EXPLAINING EVOLUTIONARY INNOVATION AND NOVELTY: A HISTORICAL AND PHILOSOPHICAL STUDY OF BIOLOGICAL CONCEPTS

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Abstract

Explaining evolutionary novelties (such as feathers or neural crest cells) is a central item on the research agenda of evolutionary developmental biology (Evo-devo). Proponents of Evo-devo have claimed that the origin of innovation and novelty constitute a distinct research problem, ignored by evolutionary theory during the latter half of the 20th century, and that Evo-devo as a synthesis of biological disciplines is in a unique position to address this problem. In order to answer historical and philosophical questions attending these claims, two philosophical tools were developed. The first, *conceptual clusters*, captures the joint deployment of concepts in the offering of scientific explanations and allows for a novel definition of conceptual change. The second, *problem agendas*, captures the multifaceted nature of explanatory domains in biological science and their diachronic stability. The value of problem agendas as an analytical unit is illustrated through the examples of avian feather and flight origination. Historical research shows that explanations of innovation and novelty were not ignored. They were situated in disciplines such as comparative embryology, morphology, and paleontology (exemplified in the research of N.J. Berrill, D.D. Davis, and W.K. Gregory), which were overlooked because of a historiography emphasizing the relations between genetics and experimental embryology. This identified the origin of Evo-devo tools (developmental genetics) but missed the source of its problem agenda. The structure of developmental genetic explanations of innovations and novelties is compared and contrasted with those of other disciplinary approaches, past and present. Applying the tool of conceptual clusters to these explanations reveals a unique form of conceptual change over the past five decades: a change in the causal and evidential concepts appealed to in explanations. Specification of the criteria of explanatory adequacy for the problem agenda of innovation and novelty indicates that Evo-devo *qua* disciplinary synthesis requires more attention to the construction of integrated explanations from its constituent disciplines besides developmental genetics. A model for explanations integrating multiple disciplinary contributions is provided. The phylogenetic approach to philosophy of science utilized in this study is relevant to philosophical studies of other sciences and meets numerous criteria of adequacy for analyses of conceptual change.

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Portions of this dissertation are *modified* segments of papers that are already published or forthcoming. I am grateful for permission to use this material here.

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The end of a matter is better than its beginning… (Ecclesiastes 7:8)

PREFACE

The present work formally falls within *philosophy of science* but the methodology is a mixture of historical investigation, philosophical analysis, and scientific research, something not necessarily observable everywhere in contemporary philosophy of science. As a result, historians may judge it as not history, philosophers may judge it as not philosophy, and scientists may judge it as not science. Alternatively, each may find too much of the *other* for their liking.

The primary animating impulse of this study is that philosophy of science research should be both relevant and useful to working scientists. Whether or not this has been achieved is an open question, although there is reason to believe that portions of it already have been. Philosophy of science is not best conceived of as a sub-discipline of 'Philosophy' but rather as a cognitive activity engaged in alongside scientists using different sets of conceptual tools, both historical and philosophical, with supplementary goals that feed back into traditional philosophical questions of epistemology and metaphysics (cf. Suppes 1990). In this sense, the line between science and philosophy of science is blurry unless analyzed sociologically in terms of its disciplinary structure in academic settings. This methodology is often referred to as 'naturalism', especially in matters epistemological, but the appropriateness of this terminology is problematic because the contrast to 'naturalism' is in many cases either too narrow or vague.

Arguably, it may be better described as 'natural philosophy', although this term is freighted with its own baggage. The American Heritage Dictionary defines it as "the study of nature and the physical universe before the advent of modern science". The online encyclopedia Wikipedia goes a little further:

> Natural philosophy is a term applied to the objective study of nature and the physical universe before the development of modern science. In other words, all forms of science historically developed out of philosophy or more specifically natural philosophy.

The difficulty with my claim and these definitions is that it would appear that one is no longer able to practice natural philosophy. And yet the present study aims to share with the philosopher-scientists of the early modern period (Descartes, Newton, Spinoza, Leibniz, Locke, Hume, Kant, *inter alia*) the simultaneous discussion of philosophical topics in light of cutting-edge scientific knowledge and research. Another relevant touchstone is in Aristotle, especially *Metaphysics* Book Epsilon (VI), because biological concepts (eye, flesh, bone, and animal) are bound up in perceptible matter and cannot be defined apart from it. This fluid movement between science and *meta*science is something that was lost over the past two centuries and needs to be fully recovered. Adequate reflection on these metaphysical and epistemological issues requires that "the results of the practitioners of the various scientific disciplines are systematically taken into account" (Glymour 1990, 69).

Invoking a justly famous discussion from the period prior to the professional divorce of science and philosophy, Herschel's *A Preliminary Discourse on the Study of Natural Philosophy* (1830), the task undertaken in this dissertation is an examination of the proper way to study particular biological phenomena as both observer and participant. The methodological combination of history, philosophy, and science necessary to accomplish this task has many attendant difficulties. A book review in *Nature* from 100 years ago apprehends some of these in a pithy manner.

> The relation of science to philosophy is, in theory, filial. It is, perhaps, no contradiction of the filial relationship that in practice it has an unfortunate tendency to run to mutual recrimination. The man of science too often ignores the philosopher, or despises him as an obscurantist who habitually confounds abstraction with generalization. To the metaphysical philosopher, on the other hand, the typical specialist in science is a variety of day labourer, dulled by the drudgery of occupational routine. Amidst such conjugal plain-speaking on both sides, it is no wonder that we hear much of what is called the divorce of philosophy and science; and yet there are many problems which for their adequate treatment surely require the combined resources of both science and philosophy.

The strategy of the present study is to make the difficult move from filial relationship *in theory* to filial relationship *in practice* (cf. Toulmin 1972, ch. 2).

1. ANALYTICAL TOOLS AND METHODOLOGY: CONCEPTS AND HISTORY

1.1. Introduction and Subject Matter of the Dissertation

The focus of this dissertation is the scientific project of explaining the origination of novel features in the history of life, *evolutionary innovations* and *novelties*, such as feathers, bone, or neural crest cells. This investigative project is one among many within the emerging area of research known as *evolutionary developmental biology* or Evo-devo (Carroll, Grenier and Weatherbee 2001, ch. 6; Gerhart and Kirschner 1997, ch. 5; Hall 1999a, ch. 13; Love 2003a, in press). What makes it worthy of special attention is that Evo-devo biologists have proclaimed it as the core of their identity as a research program.

> finding answers to what constitutes an evolutionary innovation …and how developmental mechanisms have changed in order to produce these innovations are major issues in contemporary [Evo-devo] (Olsson and Hall 1999, 612).
>
> questions on the nature of homology, …the origin of novelties and ultimately a complete understanding of evolution lie before this young discipline [Evo-devo] (Raff 2000, 79; cf. 1996, ch. 12).

Part of this identity is derived from the claim that current neo-Darwinian evolutionary theory either has ignored this explanatory project or assumed a problematic solution to it.

> [Evo-devo] may lead to a mechanistic explanation of the origin of *evolutionary innovations* and the *origin of body plans*. … Evolutionary innovations and the evolution of body plans are hard to understand in population genetic terms since they involve radical changes in the genetic/developmental architecture of the phenotype.

> …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. We think that this is the one area where [Evo-devo] will have its most lasting impact on evolutionary theory and biology in general. …we see in the problem of innovation and the evolution of body plans a unique opportunity for [Evo-devo] to develop its own independent identity as a research program (Wagner, Chiu and Laubichler 2000, 820, 822).
>
> the origination of morphological structures, body plans, and forms should be regarded as a problem distinct from that of the variation and diversification of such entities (the central theme of current neo-Darwinian theory) and that the generative determinants of organismal form must be included in any productive account of the evolution of developmental systems and organismal form in our postgenomic era (Müller and Newman 2003a, preface).

Indeed, many proponents of Evo-devo claim that the inability of neo-Darwinian evolutionary theory to explain innovations and novelties "represents one of the major gaps in the canonical theory of evolution" (Müller and Newman 2003b, 4).

These kinds of claims raise a number of questions for both historical and philosophical investigation. Beginning with historical questions, is it the case that problems surrounding the origin of evolutionary innovations and novelties were ignored or marginalized by mainstream evolutionary biology? Was this always the case or can a point in history be identified when this 'marginalization' occurred? During this historical period of time, were there any disciplinary differences, either in the extent of ignoring the problem or willingness to do so, or did it occur rapidly and uniformly? If the problem was not ignored, why is there a widespread conception of 'exclusion' among many contemporary Evo-devo biologists (and others)?

Philosophical questions that arise from these claims include, what does it mean to say that explaining innovations and novelties is 'outside the scope' or 'explanatory range' of evolutionary theory? How are we to understand the claim that the origin of evolutionary innovations and novelties is a 'distinct problem'? Supposing we can provide answers to these questions, how should we conceive of a purported 'synthesis' of neo-Darwinian evolutionary theory with developmental biology aimed at addressing this distinct problem and overcoming the explanatory lacuna? Should the study of evolutionary innovations and novelties be thought of as a distinct research program (i.e. do they constitute a distinguishable grouping of problems pertaining to particular sets of natural phenomena)? If so, how is that set of problems to be unified and what kind of demands do they place on proffered explanations of innovations and novelties, whether evidential, methodological, or otherwise? How does current Evo-devo research comport with these demands? Can we utilize the results of such historical and philosophical research to evaluate the claim that Evo-devo, as a 'synthesis', 'fusion', or 'integration' of evolution and development, is poised to make a unique contribution through a greater understanding of the causal mechanisms and processes underlying the origin of innovations and novelties?

Within these questions there at least two suggestive analytical units of philosophical interest: 'concepts' and 'problems'. Concepts come to the fore because of the centrality of EVOLUTIONARY INNOVATION and NOVELTY to Evo-devo.[1] Scrutinizing problems is relevant because understanding the origin of evolutionary innovation and novelty is claimed to be a distinct problem in evolutionary biology that Evo-devo research is poised to solve. The centrality and problematic status of these concepts takes on greater philosophical significance because of the insistence that Evo-devo constitutes some sort of 'disciplinary synthesis'.

> [Evo-devo] is not merely a fusion of the fields of developmental and evolutionary biology, [… it] strives to forge a unification of genomic, developmental, organismal, population, and natural selection approaches to evolutionary change. It draws from development, evolution, paleaeontology, molecular and systematic biology, but has its own set of questions, approaches and methods (Hall 1999a, xv)

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[1] When concepts are referred to, such as the concept of the color green or evolutionary novelty, they are signaled by the use of a 'small capitals' typographical format (GREEN; EVOLUTIONARY NOVELTY).

The dynamics of disciplinary syntheses have been of intense interest to philosophers of science, whether cognitive psychology and neuroscience, evolution and development, social science and natural science, or biochemistry and genetics (Bechtel 1984, 1986a, 1993; Bunge 2003; Burian 1986, 1993b; Darden 1991; Darden and Maull 1977; Love 2003a; Mitchell *et al.* 1997; Robert 2002; Van Der Steen 1993). This interest can be attributed to epistemological questions raised when different investigative communities or research domains are brought together, either through the creation of a new unit by integration or the production of synthetic theories or explanations that require distinct contributions from the different, autonomous domains. Some of these questions arise from problems in conceiving how such 'synthetic' or 'integrated' products are generated when the domains to be unified have differences in core problems, differences in methodology and research aims, differences in criteria of explanatory adequacy,[2] differences in disciplinary structure and function, and potentially different meanings of core terms or concepts. Related to these issues are normative questions about how to evaluate the success of such disciplinary syntheses and integrations and whether they are epistemologically favorable for structuring continuing empirical research.

To deal with these epistemological issues surrounding disciplinary syntheses in the context of the historical and philosophical questions surrounding Evo-devo's focus on innovation and novelty, I develop two specific tools related to the units of analysis already identified

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[2] 'Criteria of explanatory adequacy' refer to standards used to evaluate whether a scientific explanation of phenomena is appropriate. These criteria are not always explicit in scientific research but often operate to exclude particular kinds of explanations. They are based on the questions researchers think need to be addressed concerning the domain of phenomena under scrutiny. A common 'agenda of problems' can be agreed upon prior to possessing an adequate explanation. Two explanations may meet the criteria of explanatory adequacy but not be empirically supported to the same degree. For example, Darwin claimed in the Introduction to *On the Origin of Species* that an adequate theory of 'descent with modification' needed to address "mutual affinities of organic beings", "their embryological relations", "their geographical distribution", their "geological succession", and the exquisite nature of adaptation and "coadaptation" (Darwin 1964 [1859], 3). Natural theological reasoning addressed adaptation but not geographical distribution or succession and therefore does not meet the criteria of explanatory adequacy. Both Lamarck's theory and Darwin's theory addressed these criteria but Darwin's was better supported empirically. Thus, criteria of explanatory adequacy set a standard for appropriate explanations without necessarily being able to identify the best or correct explanation.

(concepts and problems). First, in order to understand relevant differences between biological disciplines in their attempts to explain items identified by the same terms, I develop the idea of a *conceptual cluster* to aid in isolating *conceptual* differences between these explanations. Conceptual clusters refer to how concepts are used in conjunction with other concepts in explanations, and how their deployment may be tied to methodological differences and differing criteria of explanatory adequacy among distinct disciplinary approaches. Second, in order to understand how these different disciplines might participate in a synthesis with regard to explaining evolutionary innovations and novelties, I develop the idea of a *problem agenda* as a tool for characterizing the criteria of explanatory adequacy of research domains. The goal is to specify criteria of adequacy for the phenomena under scrutiny so that normative recommendations for ongoing research, especially as found in disciplinary syntheses, can be made by facilitating judgments of adequacy or inadequacy for methods and explanations across multiple disciplines.

It is the aim of the present philosophical study to elaborate these two tools according to the above methodological emphases and then apply them to the investigation of evolutionary innovations and novelties in order to answer the previously catalogued historical and philosophical questions arising from the claims of Evo-devo practitioners. The philosophical significance of this project can be seen in relation to two particular domains: philosophy of biology and philosophy of science.

Philosophy of biology: The availability of tools that comprehend the possibilities for mediating conceptual differences across disciplines is of immediate relevance to philosophers of life science because most areas of contemporary biology are engaged in cross-disciplinary syntheses of one sort or another, especially with the spread of molecular biological techniques (Fraser and Harland 2000; Morange 1998). Similarly, the ability to precisely characterize domains by means of problem agendas helps to evaluate whether distinct research strategies are compatible or not across a wide variety of biological disciplines. Such evaluations are relevant to assessing the extent of explanatory pluralism in the biological sciences, an issue at the core of much current philosophy of biology (e.g. Dupré 1993; Ereshefsky 1992; Longino 2000; Mitchell 1992, 2002; Sterelny 2001 [1996], Wilson 2003). Moreover, this project will deepen our understanding of the concepts of EVOLUTIONARY INNOVATION and NOVELTY in evolutionary and developmental biology, which have not yet received strict scrutiny from historians and philosophers of biology.

Philosophy of science: First, the much debated problem of conceptual change stands to benefit from a new account of conceptual differences, in terms of how concepts are used in tandem, which does not rely on a particular theory of meaning or conceptual content. This may, in turn, give insight into the mechanisms of change or growth in scientific knowledge. Second, much of the discussion of problems as a unit of analysis in philosophy of science has been designed to recover the progress or rationality of scientific knowledge through history in terms of the 'problem solving ability' of theories or research programmes (e.g. Laudan 1977; Popper 1972; Toulmin 1972). More attention needs to be given to how problems *set the agenda* for research programs and, thus, are interesting units of analysis apart from any measure of progress or rationality they might offer. Third, increasing the arsenal of tools that facilitates the diagnosis of conceptual differences in disciplinary syntheses, and whether these differences are complementary or mutually exclusive, enhances our comprehension of the epistemological character of multidisciplinary interactions, a topic of interest to many philosophers of science.

The present chapter is devoted to developing the concept-related analytic tool that I have termed *conceptual clusters*, as well as a method for the historical study of philosophical issues that has been termed the *phylogenetic approach to philosophy of science* (thus the subtitle, 'concepts and history'). Section 1.2 delineates the reasons for focusing on the differences in the joint deployment of concepts in the offering of scientific explanations and works out the basic ideas concerning conceptual clusters. Section 1.3 describes the phylogenetic approach to philosophy of science, especially in regard to using the new tool of conceptual clusters. Section 1.4 relates conceptual clusters to the broader literature on concepts and conceptual change, situating it with respect to a variety of other existing philosophical projects, including historical investigations of concepts. In closing I sketch the road ahead through a synopsis of the philosophical methodology in relation to the remaining chapters of the dissertation.

1.2. Tracking Conceptual Differences in Explanations: Conceptual Clusters

1.2.1. Methodological Considerations

The methodology adopted to develop a tool for tracking conceptual differences follows two existing lines of argument in philosophy of science. The first is a focus on scientific *practice* prior to an analysis of the *nature* of scientific knowledge, illustrated in Mitchell's discussion of the pragmatic dimensions of scientific law (Mitchell 1997, 2000). Instead of concentrating on what does or does not count as a law that could genuinely enter into a scientific explanation, she draws attention to the fact that scientists (particularly biologists) do *use* generalizations in explanations, regardless of whether they are universally applicable as in traditional conceptions of scientific laws. This leads to a fruitful exploration of the different kinds of generalizations used by biologists and thus a different analysis of the issue of how 'laws' enter into scientific explanations. The methodology begins by dissecting a feature of scientific practice and then moves to its characterization; i.e., from how scientists *use* generalizations to an analysis of what those generalizations might *represent* (cf. Toulmin 1972, 157ff).

Second, many scientific concepts tend to be *natural kind* concepts (Fodor 1998),[3] which can be understood as homeostatic property clusters (*not* necessary and sufficient conditions) that evolve over time or historical essences (relationally defined) with detectable counterfactual force (Boyd 1991, 1999; Griffiths 1999). The key consideration is the role these natural kinds play in the inferential *practice* of scientists, where their projectability to undiscovered instances is licensed by the current best theory they are embedded within. This 'contextual embedding' has also been shown to play a critical role in the function of everyday natural kind concepts (Keil 1989; Murphy and Medin 1999 [1985]). If theorists aim to use projectable categories (concepts) for explanatory and inductive purposes and that projectability is determined by a theoretical context (cf. Koslowski 1996; Koslowski and Thompson 2002), then attention to that context rather than just the concept itself is critical for understanding the *use* of concepts. The cooperative utilization of concepts in relation to a primary concept could underwrite a license to project the concept onto new instances. This dimension of concept use falls outside of the intense attention to reference within philosophy of science, which does not attempt to capture the role of conceptual context in coordinating reference determination for scientific concepts.

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[3] I will use the locution 'theoretical (kind) concepts' to avoid issues of whether their grouping of instances is natural (or 'real') and whether or not non-scientific concepts can be investigative (cf. Brigandt 2003; LaPorte 2004). I also avoid 'empirical concept' because it is too close to 'perceptual concept' (such as RED), which is very different from the concepts of EVOLUTIONARY INNOVATION and NOVELTY at the center of the present study.

When we consider how scientists *use* concepts (including but not limited to theoretical kind concepts) in the offering of explanations, a salient if often overlooked feature is that explanations involve *multiple* concepts. The theoretical context of a concept can be understood in terms of the other concepts jointly utilized in scientific explanatory practice.[4] For example, if an ecologist is trying to explain the decline in population size of a particular species, any explanation will involve a variety of concepts, including species concepts for the relevant taxa, abstract descriptive concepts (e.g. POPULATION or GUILD), and causal concepts (e.g. COMPETITION), to mention a few. This serves as our core feature of scientific practice from which to begin developing the tool of conceptual clusters: no scientific concept *functions* in isolation in scientific explanations and is always nested within a set of relations with other concepts.[5] But this contextual 'functioning' can be made more precise. Usually a particular concept is at the *center* of an explanatory project, in the sense that it represents or refers to a grouping of natural phenomena that poses particular questions (i.e. a theoretical kind concept). I label this the *explanatory target* concept. In addition to concerns about the empirical adequacy of concepts, we can recognize a set of other concepts that are jointly deployed when offering an explanation of whatever phenomena the explanatory target concept represents. Questions can be asked about the role these other concepts play together, as a *cluster*, in the scientific reasoning process referred to as an explanation of natural phenomena.[6] This is a very general feature of

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[4] This is not the only way to flesh out the idea of theoretical context. Other decompositions may be fruitful but are not considered here. A concern might arise that attention to concepts keeps scientific knowledge rather than practice (such as experimental, technological, or social practices) at the forefront, therefore short-circuiting this type of approach (Laudan 1993; Pickering 1992). This is only true if the behavior of concepts cannot be considered a social epistemic practice. Some historians and sociologists have drawn attention to 'conceptual practice', particularly with respect to mathematics (Pickering and Stephanides 1992), and 'conceptual practice' seems quite reasonable as a domain of 'practices' (McGuire and Tuchanska 2000, ch. 2; Prinz and Clark 2004; Rouse 1996, 2003).

[5] Arguably, this is a general feature of concept use: "Adequacy in concepts is tested by whether their employment makes stable judgment possible. But no judgment employs only one concept" (Millikan 2000, 105).

[6] A feature of scientific concept use akin to this was recognized previously by some philosophers of science: "systematic import is another indispensable requirement [for scientific concepts]–so much so that the empirical

scientific explanation and one that directs our attention to the isolation of conceptual differences in terms of the conceptual context of an explanatory target concept by identifying conceptual clusters. Notice that this relational structure among scientific concepts is distinct from the issue of how perceptual concepts undergird or provide empirical scaffolding for complex theoretical concepts. This latter concern, which might be called the *vertical* relationship among concepts, was a critical point of discussion in logical empiricist philosophy of science, especially as it arose out of discussions of operationism.[7] However, the feature of scientific practice in view here is the *horizontal* relations among scientific concepts as seen in the practice of offering explanations of natural phenomena.

1.2.2. Explicating Conceptual Clusters: Toolkits

In order to explicate the notion of a conceptual cluster two metaphors can be invoked. The first is the notion of a conceptual *toolkit*. Different research traditions or scientific disciplines can be thought of as having a conceptual toolkit, which includes all of the concepts that have been cobbled together or forged *de novo* in tackling one or more empirical or theoretical problems. Some of these tools will be central to the research tradition, having been invented or originally co-opted and substantially modified, whereas others are 'loaners', borrowed from distinct research disciplines where they find their substantive grounding (cf. Klein 1990, ch. 5, 1996, ch. 3; Kockelmans 1979a; Maull 1977, 149ff). A conceptual toolkit of a

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interpretation of theoretical concepts may be changed in the interest of enhancing the systematic power of the theoretical network" (Hempel 1966, 96-7; cf. Carnap 1956; Hempel, 1952).

[7] Hempel aptly summarizes the relevant issues between logical empiricism and operationism. "Operationism, in its fundamental tenets, is closely akin to logical empiricism. Both schools of thoughts have put much emphasis on definite experiential meaning or import as a necessary condition of objectively significant discourse, and both have made strong efforts to establish explicit criteria of experiential significance. But logical empiricism has treated experiential import as a characteristic of statements—whereas operationism has tended to construe experiential meaning as a characteristic of concepts or of the terms representing them—namely, as their susceptibility to operational definition" (Hempel 1965 [1954], 123).

discipline will thus be the total pool of concepts from which a conceptual cluster can be formed in the process of offering a scientific explanation. Its contents are subject to change over time and will differ depending on when historians and philosophers of science observe them.

Three features are in focus for this analogy. First, owned versus borrowed tools picks out differences of origination and mastery. Although borrowed tools can eventually become mastered, their use *as borrowed* indicates that they are not central for the tasks undertaken by a disciplinary approach. If they become central, the tools can be permanently co-opted. Some concepts are central to particular research traditions but many times concepts must be borrowed when offering particular explanations. Concept 'borrowing' is ascertained by investigating what is assumed with respect to the concept and whether this is obtainable from the conceptual toolkit of the scientific discipline. For example, if a developmental geneticist attempts to explain the origin of vertebrate jaws using the higher taxa grouping AGNATHAN FISHES, this concept is borrowed rather than owned because its meaning presupposes systematics and paleontology conceptual resources and methodology. In contrast, *for the same target of explanation*, developmental geneticists own the concept BONE MORPHOGENETIC PROTEIN because the meaning is derived from material available within their conceptual toolkit. This feature is important for assessing the need of conceptual resources from different research traditions for specific problems, drawing attention to the conditions that demand interdisciplinary explanations.

Second, there are more tools in the toolkit than are needed to solve any particular problem. Scientific disciplines often have multiple empirical and theoretical problems in view that demand the use of different sets of tools at different times. Third, toolkits have a diversity of component types (wrenches, screwdrivers, hammers, etc.) that can be used for a variety of tasks. These tool types are designed for particular purposes and together can be extremely useful in executing complex building or repair projects. Similarly, scientific disciplines have a diversity of concept types available for ongoing investigation of the natural world, which is of particular importance for understanding conceptual clusters. What kinds of components appear in conceptual clusters for scientific explanations?[8] I propose the following as a non-exhaustive list of abstract concept 'types' routinely found in explanations offered by scientists and composing the conceptual toolkits possessed by different scientific research traditions.

- *Entity* concepts: a variety of physical instantiations of bounded things, although without a presupposition that the individuation of these entities is theory neutral.
- *Activity* concepts: behaviors that entities are involved in but that do not reduce to properties of the entities themselves (Machamer, Darden and Craver 2000).
- *Property* concepts: entities and activities can be ascribed properties of various kinds (e.g. dispositional properties).
- *Relation* concepts: these can be relations of space, time, or cause.
- *Process* concepts: generalizations derived from accepted scientific descriptions or explanations that are used to license particular inferences (entities and activities with properties in particular relations to other entities and activities).

Although the terminology for this taxonomy is unique, some of the distinctions among concept types roughly map to distinctions theorized by psychological researchers, such as noun (*entities*) versus verb (*activities*, nominalized) concepts or reasoning role differences between attributive (*properties*) and connective (*relations*) concepts (Medin, Lynch and Solomon 2000). Thus, at a very abstract level of characterization we can illustrate a possible scientific explanation using these toolkit categories: the origination, existence, or transformation of a particular ENTITY with

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[8] I am assuming explanations are causal or mechanistic (Glennan 2002; Lipton 2004; Machamer, Darden and Craver 2000; Lewis 1993 [1986]; Ruben 1990; Salmon 1989, 1998; Woodward 2003). The meaning of 'cause' is a question beyond this study (Cartwright 2004; Hall and Paul 2003). The role of causal information and assumptions plays a key *contextual* role in reasoning processes (Koslowski 1996; Koslowski and Thompson 2002).

specific PROPERTIES is ascribed to the ACTIVITY of a suite of ENTITIES that exhibit a set of PROPERTIES and bear RELATIONS (e.g. sufficient causal ones) to the ENTITY to be explained. A variety of evidence (observational or experimental) will support claims about the ENTITIES, ACTIVITIES, PROPERTIES, and RELATIONS including appeals to existing PROCESSES discerned from other research endeavors. Two short examples help flesh out this abstract characterization.

First, consider a question from comparative biology: why are particular skeletal elements shared among vertebrate species? Answer: The skeletal elements [ENTITIES] are shared [RELATION - space] because the common ancestor of vertebrates [ENTITY] instantiated them [PROPERTY] and they were inherited [RELATION – causal] in subsequent vertebrate lineages [ENTITY]. The explanation is supported by features [PROPERTIES] of the skeletal elements [ENTITIES], such as shape, relative position to other skeletal elements, or histology [PROPERTIES]. These are obtained through observation of the embryological origin and adult location and shape of the skeletal elements, as well as tissue histology observed microscopically in sectioned specimens. This explanation is also favored because of other studies of homology, which have established similar links by similar means [PROCESS], as well as providing conditions for excluding alternative explanations such as analogy.

Second, consider a question from contemporary molecular neuroscience: why does a neuron [ENTITY] fire or release its action potential [ACTIVITY]? A neuron [ENTITY] fires [ACTIVITY] when ion channel protein complexes [ENTITIES] open [ACTIVITY] successively [RELATION - time] along [RELATION – space] an axon [ENTITY] and allow a particular kind of ion [ENTITY] to enter the cell [RELATION – space], propagating an electrical impulse [ACTIVITY] directionally [RELATION – time and space], which results in the release [ACTIVITY] of neurotransmitters [ENTITY] across [RELATION – space] a synapse [ENTITY]. (Some) evidence for this explanation is garnered by patch clamp techniques that measure the change in electrical potential, molecular genetic analyses that disrupt ion channel function, and biochemical analyses that manipulate ion concentrations. Other considerations include the 'routine' behavior of ions and the stimulatory effect of an electrical impulse [PROCESSES].

These examples highlight conceptual context component possibilities and carve out an initial expectation for the isolation of components (or 'tools') in a conceptual cluster. There is nothing privileged about the forms offered as examples. Scientists may want to explain the existence of an activity rather than an entity and the homology example contrasts with the neuronal firing example in the citation of activities as key components of the explanation. I am not proposing an explanatory *schema*, something that requires abstract placeholders to receive concrete values.[9] Returning to the toolkit metaphor is helpful. Looking inside the conceptual toolkit of a research tradition may give you an idea of the concepts used by scientists in offering explanations but it will not provide concrete guidance as to which concepts need to be jointly deployed in a specific explanation. This requires a prior knowledge of what is in need of explanation. A particular number of concepts or the presence of each concept 'type' is not required for a satisfactory scientific explanation. The satisfaction of criteria of explanatory adequacy is a function of the *explanandum* in focus for the scientific discipline. In the present study, the explanatory target concept is EVOLUTIONARY INNOVATION or NOVELTY. Conceptual clusters are then understood as the conceptual context of this explanatory target concept, which

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[9] This does not mean that schemas cannot be constructed but the goal is to attend to conceptual differences in explanations, which are often eliminated when attempts at schematization are undertaken.

refers to activities or entities present in descendant species but absent in ancestral species and the key burden is explaining their historical origin within particular lineages.[10]

Recognizing that the group of concepts used is specifically related to the target of explanation in view emphasizes that it is not the *formal* properties of the concept *types* in relation to one another that determines their significance in an explanation. Rather, it is the *material* properties of the concept *tokens* in relation to one another that is relevant for assessing the conceptual context for a particular explanation (cf. Gärdenfors 2000; Keil 1989; Koslowski 1996; Koslowski and Thompson 2002; Murphy and Medin 1999 [1985]).[11] There is nothing about having a wrench, screwdriver, and hammer in one's toolkit that provides an account of how they will be jointly utilized. The need to fix a leaky sink is critical for knowing which tool tokens (such as a pipe wrench) will be utilized and in what order or fashion. In accordance with the methodology adopted, documenting a conceptual cluster that utilizes particular concepts from a disciplinary toolkit will always be a function of observing how scientists are attempting to explain something and applies to 'presentations' of explanations found in journal articles, books, or other formats (Griesemer 1984).

The emphasis on the material rather than formal properties of concepts in relation to one another is *methodologically analogous* to some accounts of conceptual content, where material rather than formal inferences play the key role (cf. Brandom 1994, 2000; Sellars 1953, 1963 [1954]).[12] What licenses inferential transitions or, weaker, establishes relations among concepts,

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[10] As will become clear in the next chapter, I advocate using NOVELTY to refer to the origin of new entities and INNOVATION to refer to the origin of new activities, but the distinction is not drawn here. Justification for this conceptualization of evolutionary innovations and novelties is found in Chapter 2.

[11] The difference here between a concept *type* and concept *token* refers to the distinction between *entity* concepts (concept kind) and AXON (concept token) as an entity concept, *not* a distinction about whether a concept is found in an individual or used at a particular juncture versus present in a wider community of concept users.

[12] "As examples, consider the inference from "Pittsburgh is to the West of Philadelphia" to "Philadelphia is to the East of Pittsburgh," the inference from "Today is Wednesday" to "Tomorrow will be Thursday," and that from "Lightning is seen now" to "Thunder will be heard soon." It is the contents of the concepts *West* and *East* that make

are facts about the world as currently understood by scientific research, which reiterates the historical aspect of documenting and evaluating conceptual clusters.[13] A similar point has been recently made with respect to theories of induction, where the 'goodness' of inductive inference is not dependent on formal properties of the inference form but rather the material properties of the things the inductive inference concerns (Norton 2003). Relations in conceptual clusters are not grounded, for example, in how entity concepts are related to property concepts but in what entities or properties are actually involved (such as neurons). In the experimental psychology literature on concepts, a cognate of this behavior is referred to as 'domain specificity' (Carey and Spelke 1994; Hirschfeld and Gelman 1994; Medin, Lynch and Solomon 2000).[14]

The toolkit metaphor has limits in explicating conceptual clusters. First, the conceptual cluster itself is only a subset of the members of a conceptual toolkit and thinking about the toolkit itself does not illumine the material structure of the concepts within a cluster in particular explanations. Second, although a toolkit differs depending on the historical juncture at which it is observed, there is no trace of this historical variation in the toolkit itself. Whether a screwdriver was added first or last and for what reason is not detectable by examining the contents of the toolkit alone. An examination of the problems that tools have been used for is needed, which again directs us to the clusters themselves rather than the toolkit. Finally, the

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the first a good inference, the contents of the concepts *Wednesday*, *Thursday*, *today*, and *tomorrow* that make the second inference correct, and the contents of the concepts *lightning* and *thunder*, as well as the temporal concepts, that underwrite the third. Endorsing these inferences is part of grasping or mastering those concepts, quite apart from any specifically logical competence" (Brandom 1994, 97-98).

[13] "Grasping a concept is mastering the use of a word—and uses of words are a paradigm of the sort of thing that must be understood historically. In this sense even concepts such as *electron* and *aromatic compound* are the sort of thing that has a history. But they are not *purely* historical. For the proprieties governing the application of those concepts depend on what inferences involving them are *correct,* that is, on what *really* follows from what. And that depends on how things are with electrons and aromatic compounds, not just on what judgments and inferences we endorse" (Brandom 2000, 27).

[14] Domain specificity is distinct from the aspect of concepts I am drawing attention to here because even though both perspectives share an emphasis on 'domain specific' behaviors of concepts, the material rather than formal behavior of concepts in view usually is not included under the heading 'domain specificity' nor does it connect with the emphasis on innateness in discussions of domain specificity (Hirschfeld and Gelman 1994, 2324).

toolkit metaphor does not capture the necessary joint deployment of concepts in explanations, as certain ‘mechanical’ problems require the use of only a single tool. Scientific explanations demand that multiple concepts be in play. These limitations lead us to select another metaphor to explicate the nature of the cluster itself, remembering that explanatory target concepts will correspond to the natural phenomena being explained, that the material relations among the concept tokens are more important than formal relations among concept types, and that having an explicit trace of the historical aspects of conceptual toolkits is desirable.

1.2.3. Explicating Conceptual Clusters: Neighborhoods

A natural and widespread metaphor that has been used for relations among concepts is that of a *network*. This metaphor is less helpful for present purposes because there is no analog of the diversity of component types picked out in the toolkit metaphor. The imagery of the nature of relations between concepts in a network is quite minimal, emphasizing formal relations (a network connection is literally a ‘line’ that makes contact with two particular ‘nodes’), and there is no explicit trace of historical changes in networks over and above that available with the toolkit metaphor. Despite surface similarities between ‘clusters’ and ‘networks’, a different metaphor is required to explicate the phenomena of scientific practice we have isolated.

One metaphor that can help explicate the desired features of conceptual clusters lacking in the toolkit metaphor is that of a *neighborhood*, which provides richer descriptive associations. First, neighborhoods often have a central focus, especially as found in ‘town centers’ of more distant history where religious or civic buildings were spatial foci. This corresponds to our explanatory target concept around which a conceptual cluster is formed. In connection with this, a neighborhood or town can be thought of as a joint but temporally extended response to the problem of how to structure a communal life. Second, a neighborhood has a diversity of component types. Neighborhoods are composed of living spaces (houses or apartment complexes) commercial spaces (grocery stores, hardware stores, pharmacies), recreational spaces (parks), civic spaces (court and government buildings), and religious spaces (churches, synagogues, or mosques). There is no necessary relation among these component types (e.g. civic space may or may not abut living spaces) except as is established with respect to the community aims of structuring the neighborhood (e.g. through zoning laws). The actual relations among the component tokens, which is a reflection of both functional needs and historical contingencies, is the structure of the neighborhood, just as differences of particular conceptual cluster members in relation to the explanatory target concept establish the relations among conceptual cluster components. The spatial relations among these component tokens are an explicit trace of the historical development of a neighborhood (although demolition and rebuilding can erase this).

As noted, conceptual clusters are reconstructed from ‘presentations’ of explanations found in the scientific literature and should be recognizable by participant scientists (Griesemer 1984). Conceptual clusters, similar to neighborhoods, can exhibit their history through descent with modification by a variety of inheritance mechanisms, and thus are subject to an evolutionary-type analysis (Griesemer 1984, 103). Conceptual variation and change can be documented over historical periods of time for conceptual clusters, especially in the sense of different structural relations concerning the kinds of evidence marshaled or causes appealed to in favor of a particular explanation in the problem domain. The spatial relations feature of actual neighborhoods finds its analogue in the proximity relations of particular concepts representing evidence and causes that underwrite preferred explanations of the explanatory target concept phenomena, where ‘close’ corresponds to greater role and ‘distant’ to a lesser role.

A final feature of neighborhoods is helpful for analogically explicating conceptual clusters; neighborhoods can be found in periods of relative stasis or dynamic change. Often this is reflected in the amount of new construction and influx (or efflux) of people residing in a particular neighborhood. Conceptual clusters can display an analogous ‘equilibrium state’ or lack thereof, both in terms of its members and their relations.[15] Equilibrium states can be disturbed through input from a variety of contextual factors, as well as internal tensions in a theoretical framework. Returning to a previous equilibrium state after disturbance or obtaining a different equilibrium may entail rearranging relations among concepts, severing connections between concepts, removing a constituent concept, or drawing tighter links between previously disparate notions. Therefore we can to recover an operational notion of conceptual functioning in science being *stable* over time, as well as subject to *change*, which is cashed out in terms of changes in conceptual clusters and their various equilibrium states. The phenomenon of equilibrium states in conceptual clusters offers a new characterization of epistemic changes that occur in scientific theorizing. Equilibrium state disturbance is often correlated with larger upheavals in the theoretical foundations of a science. It also allows for a finer grained analysis of so-called ‘normal science’ (Kuhn 1962; Nickles 2000, 2003), providing ways to dissect

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[15] The notion of equilibrium is inspired by comments of Donald Davidson, although my use departs from the intent of his remarks in their original context. “Concepts such as that of length are sustained in equilibrium by a number of conceptual pressures” (Davidson 1980, 221). Other philosophers have made similar observations: “Concepts and statements are indeed stable, but this stability is created by an interdependent set of practices, a field, or style of reasoning, whose existence confers a specific role or function on our words, allows them to exhibit certain “strategic potentialities” (Davidson, A. I. 2001, 187; cf. Hacking 2002b). The idea of conceptual cluster equilibrium states is meant to more precisely capture how this conceptual stabilization might behave over time in scientific research with respect to the offering of explanations (rather than entire theoretical frameworks).

changes that do not indicate ruptures or discontinuities.[16] Considering equilibrium states of conceptual clusters reiterates the historical dimension of conceptual use in terms of the stability or instability of relations among concepts as they are used in explaining natural phenomena at distinct periods of time.

Returning to our comparative biology example, the spatial center or rationale is the phenomena of similarity among biological units, such as skeletal elements in vertebrates. The material relations in focus pertain to particular concepts taken as evidence in favor of a causal explanation of HOMOLOGY (explanatory target concept), notably those supporting that the common ancestor of vertebrates [ENTITY] instantiated them [PROPERTY] and transmitted [RELATION – causal] them to subsequent vertebrate lineages [ENTITY]. These include the shape, relative position to other skeletal elements, embryological origin, or histology [PROPERTIES] of the skeletal elements [ENTITY]. Historically, these different properties alternated in how 'close' they were to the evidential core of a causal explanation of homology. For example, embryological origin originally provided the best evidence for homology but it later became more 'distant' in the conceptual cluster because of discoveries showing that homologous features could have distinct developmental origins (Laubichler 2000). More recently, a number of traditional explanations of homology with conceptual clusters in equilibrium states have been upset by the concept GENE EXPRESSION, which is now understood as a property of species subject to comparison as a result of a distinct research tradition, molecular developmental genetics.

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[16] Kuhn has argued that the former is the explanatory target of historical philosophy of science: "For the philosopher who adopts the historical perspective, the problem is the same [as for historians]: understanding small incremental *changes* of belief" (Kuhn 2000 [1992], 112).

1.2.4. A Comparison

We now have developed the tool of a conceptual cluster in terms of the toolkit and neighborhood metaphors along the following lines of reasoning. Scientific disciplines or research traditions have a variety of concepts of different types available (some owned, some borrowed) when attempting to explain natural phenomena, although only a subset of them is usually deployed. This subset, a conceptual cluster, is identified in explanation presentations offered by scientists through an explanatory target concept, which refers to the suite of natural phenomena that pose problems in need of explanation. These clusters have several features analogous to neighborhoods. The relations among the concept tokens are dictated by the nature of the problem they are utilized to tackle rather than abstract or formal considerations among the concept types. These relations bear evidence of a historical process whereby they originated. Conceptual clusters also exhibit periods of stasis and change, similar to neighborhoods, which signals the nature of epistemic activity occurring over time with respect to the problem (in relation to which the cluster is formed).

It is illuminating to compare what I term ‘conceptual clusters’ with an account of the relations among scientific concepts offered by another philosopher of science (Thagard 1992; cf. Thagard 1999). First, Thagard’s focus is on revolutionary changes in scientific epistemic units, particularly concepts, such as in the transition from Newtonian mechanics to a theory of relativity. The account of conceptual clusters requires no privileging of a particular kind of epistemic change in science, revolutionary or otherwise. Second, the unit of analysis for Thagard is a ‘system of concepts’, which is conceived of as a hierarchically related network of concepts exhibiting part and kind relations. Concepts are complex representational structures similar to ‘frames’, “symbolic structures that specify for a concept various slots and default values for a slot" (Thagard 1992, 24; cf. Thagard 1988), with a focus on hierarchical part and kind relations as well as rules for use in explanations and theories (cf. Barker, Chen and Andersen 2003; Chen and Barker 2000; Nersessian 2002, 2003). Conceptual clusters are a finer grained unit of analysis than Thagard's systems of concepts, as conceptual clusters pertain to the *subset* of concepts jointly deployed in explanations of natural phenomena. For any particular theoretical framework or scientific discipline their 'system of concepts' (or conceptual *toolkit*) is more encompassing than a conceptual cluster and likely is constitutive of that particular research tradition. Conceptual clusters are modeled on the *use* of concepts and need not represent akin to frames (or any other account of concepts). They do not require that the relations among concepts be understood primarily as part/kind hierarchies (though they include this kind of behavior), nor do they imply explanation schemas for particular domains of inquiry (cf. Thagard 1999, ch. 2).

That conceptual clusters are derived from observing the use of concepts rather than elucidated through an analysis of the nature of concepts is a critical difference between Thagard's account and my own, as he derives their categorization use from an account of their representational structure as 'frames'. Thagard's commitment to an account of what concepts are, along with his historical investigations of particular revolutions, leads him to construe different kinds of conceptual *change* as more or less significant. The adding of new instances under a concept has little impact while the reclassification of things originally considered to fall under a concept (or a change in the hierarchical relationship among concepts) is the substance of conceptual revolutions. Because conceptual clusters do not have assumed formal relations among concept kinds (e.g. hierarchical part/kind), there is no requirement to treat one kind of conceptual change as more significant than another. The significance of changes in conceptual clusters depends on the material relations of these concepts in terms of the evidence supporting a causal explanation of the natural phenomena under scrutiny. Additionally, Thagard's treatment repeatedly deploys a network metaphor for concepts, which, as we have observed, is not helpful for explicating several important features of conceptual clusters.

1.2.5. Isolating and Characterizing the Significance of Conceptual Clusters

Two basic questions must now be addressed concerning conceptual clusters: (1) how is the conceptual cluster to be operationally delimited, and (2) what is the significance of 'activity' within a conceptual cluster.[17] First, we treat their isolation in explanation presentations. The crux of my account of how conceptual clusters will be isolated has already been sketched: conceptual clusters are identified through attention to explanations offered for natural phenomena represented by explanatory target concepts. Other options for picking out clusters are available, though not desirable in this context. One could appeal to inferential connections to define conceptual clusters, akin to some accounts of conceptual content (e.g. Brandom 1994, 2000). This choice is unfavorable because it unnecessarily saddles the tool of conceptual clusters with a controversial philosophical semantics. The aim was to generate a concept related tool that picks out conceptual differences without relying on specific assumptions about the nature of conceptual content or meaning. That multiple concepts are deployed in scientific explanations does not tell for or against existing theories of conceptual content.

A different approach that is semantically noncommittal understands relations among concepts through statistical patterns of word co-occurrence. A 'Hume-Condillac machine' in

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[17] These questions are analogous to those posed for accounts of conceptual *content* that emphasize the importance of connections between multiple concepts. For example, Fodor argues that "[i]f you want to take the Quine picture seriously for the purposes of a theory of concepts, there are two problems you have (a) to distinguish, and (b) to solve: namely, how are theories individuated; and, given individuation conditions for theories, how are concepts constituted by the theories that embed them?" (Fodor 2000, 363). Thus, for conceptual clusters we are asking how they will be isolated and what their import might be.

sociological studies of science aims to identify terminological co-occurrence without a bias from association types determined in advance, such as 'student of' (Teil and Latour 1995; cf. Callon, Law and Rip 1986).[18] This association machine purports to isolate nonrandom associations of word occurrences via the trawling of texts and archival material. Although this approach may be enlightening, three reasons prevent its use here. First, the common utilization of the terms 'innovation' and 'novelty' make it likely that irrelevant aspects of the scientific literature will come into purview. For example, a keyword search on novelty turns up articles primarily related to research in psychology on novelty-seeking behavior. Notice that if we added 'evolutionary' as an association type, we violate the methodology and likely miss interesting instantiations of the concepts that do not utilize the modifier. This is not simply a distraction (because there are larger numbers of researchers working in psychological studies of novelty-seeking) but indicates a lack of statistical power for a study of evolutionary innovation and novelty due to the relative paucity of documents available for analysis. This is exacerbated when moving further into the past with historical investigations.[19]

The second problem concerns the fact that these groupings will be conceptual context types rather tokens. Because we are interested in whether conceptual clusters play an epistemologically interesting role in explanations, especially with respect to disciplinary differences, attention to tokens is preferable. The construction of types may obliterate interesting but statistically insignificant variation. Lastly, word co-occurrence algorithms depend on proximity measures (groupings reveal words that are literally closely associated in texts) but presentations of theories are often diffuse in scientific texts (Griesemer 1984). Thus, important

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[18] There is currently an ongoing proliferation of these types of analysis, as seen in a recent PNAS symposium (Shiffrin and Börner 2003) and reviewed elsewhere (Börner, Chen and Boyack 2003).

[19] Also, we are inherently interested in conceptual co-occurrence in particular practices of scientists (offering explanations), which implies that the detection of nonrandom terminological networks of co-occurrence may be utterly uninformative due to an absence of any relation to this focus on a particular conceptual practice.

connections may fall below the radar of this kind of methodology, which are relevant for understanding how concepts operate together in explanations of natural phenomena.

The solution to isolating conceptual clusters adopted here lies in focusing on the explanatory aims of scientists. What delineates the co-occurrence of concepts in scientific explanatory projects is a *problem agenda*. The primary burden of the next chapter is to explicate this notion but a few of its aspects can be introduced. A problem agenda usually surrounds a suite of phenomena identified under a common rubric, often an explanatory target concept, which is in need of explanation (e.g. ADAPTATION). Problem agendas are abstract conglomerations of the outstanding 'big' questions that scientists deal with concretely through research questions addressed to their preferred systems of investigation using particular methodologies. Although scientists recognize different problem agendas, most research groups tackle more than one problem agenda simultaneously and thus there is potential for conflation of the explanatory burden attending different problem agendas. The likelihood of conflation increases when different disciplines are attempting to work on questions in the same putative problem agenda. Therefore, a clear statement of the problem agenda, how it is distinct from other problem agendas, and the criteria of explanatory adequacy for the problem agenda need to be articulated, especially for multidisciplinary activities (see Chapter 2 for discussion).

Explanatory target concepts pick out problem agendas and anchor the search for relevant, jointly deployed concepts that compose a cluster. This does not prevent concepts found in a particular cluster from playing a role in *different* conceptual clusters with respect to distinct problem agendas. Returning to the toolkit metaphor, various combinations of existing concepts can be deployed in distinct combinations to deal with different problems. Highlighting a particular concept that is central to a particular problem agenda over a period of history will likely reveal adjustments or alterations in conceptual clusters with respect to answering particular problem agenda questions. Success on particular research questions in contrast to recalcitrance in others may change the way an explanatory project is understood. New technologies or empirical discoveries can shift the emphasis (i.e. which concepts are 'close' or 'far') to a subset of conceptual members in a particular cluster, introduce new concepts, or encourage the neglect or removal of other member concepts.[20]

There may remain a worry that one can isolate a conceptual cluster through attention to problem agendas. On what basis can we be confident that particular concepts are *not* a part of a cluster involved in the practice of offering an explanation? The first component of a response is to reiterate that conceptual clusters are identified in explanation *presentations* and thus there is no hidden component lurking unavailable to be identified. Although an analysis of the behavior of conceptual clusters may direct our attention to implicit notions involved in an explanatory project, this is something secondarily identified. The second aspect of a reply to this worry is found in the practical limitations of researchers. Given a particular explanatory target concept connected with a problem agenda, researchers are only interested in a small set of research questions that bear on this domain.[21] Characterizing the problem agenda is the key task in this respect because it makes explicit what is in need of explanation and whether or not particular conceptual clusters observed in explanation presentations are adequate when used to address research questions. Determining the independence of these sets of questions on existing theoretical grounds is the prerequisite needed to delimit a conceptual cluster because clusters

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[20] Scientific concepts are often introduced to refer to collections of entities or phenomena that are initially thought to demand an independent, or at least distinct, explanation (if not theoretical framework); i.e., as 'investigative kinds' (Brigandt 2003; Griffiths 2004; see also, Section 2.1, above). Similarly, scientific concepts are sometimes eliminated or bifurcated when these collections of entities are ascertained to be artifacts or artificially grouped.

[21] Bromberger has discussed the issue of 'rational ignorance', which has as its premise our inability to focus on answering more than a subset of genuine questions (Bromberger 1992, 128-169). "People can and do choose to find out certain things and to remain ignorant about others. And they don't all make the same choices, even when the same choices are available to them" (128).

contain concepts invoked in the practice of offering answers (explanations) to the questions in the domain of problem agendas. Evidence of this independence is observable in the fact that explanation presentations are offered distinctly in scientific articles and other publicly accessible formats. The delineation and differentiation of different problems in scientific reasoning reflects a fundamental component of cognitive practice in science and has been obliquely recognized by cognitive psychologists and other researchers concerned with conceptual function.[22]

Assuming conceptual clusters can be isolated there remains the issue of their import. Our primary goal was to develop a tool that could track conceptual differences in scientific explanations arising from different research traditions in order to adjudicate relevant contributions to explanations of evolutionary innovations and novelties in the context of Evo-devo. Delineating the conceptual cluster in use around a particular explanatory target concept allows one to make explicit what other concepts are being deployed for the purposes of scientific explanation. Having explicated a particular pattern observable in the *use* of scientific concepts, what is the *nature* of this pattern, or, what does it *mean*? One way of answering this question is with respect to the semantics of conceptual content but our tool was designed to track conceptual differences apart from particular philosophical accounts of conceptual content or meaning. How are these differences in the conceptual cluster of an explanatory target concept found in scientific explanations to be understood? Do differences in clusters lead to differences in the *meaning* of the explanatory target concept, or other member concepts? Although it is tempting to answer

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[22] "It is not clear that 'explanatory holism' has to be true, but even if it were, it doesn't follow that distinct clusters of explanations are not powerfully linked with different concepts. … Explanatory beliefs are not distributed evenly in the web of understanding. They form tight, richly structured clusters that then have sparse links to other clusters. Beliefs about the mechanics of solid objects, for example, are richly structured and tightly interconnected, but their connections to the cluster of beliefs about minds are comparatively few" (Keil and Wilson 2000, 314).

based on philosophy of language assumptions,[23] conceptual clusters will be most powerful when we remain noncommittal about the general semantic ramifications of their differences.

A natural objection concerns whether a semantically noncommittal notion of conceptual context is toothless when it comes to the evaluation of conceptual differences in scientific explanations. I think not for three primary reasons. First, the existence of abundant analyses of single concepts without sufficient attention to their *conceptual* contexts in the activity of scientific explanation means we simply do not have a good idea of how conceptual clusters operate. Until we are better cognizant of their operation, it is premature to say that conceptual clusters are uninteresting without being linked to an account of conceptual content. Second, it allows for a new way of talking about conceptual *change* in the face of conceptual stability. If it is determined that the explanatory target concept under scrutiny and other conceptual cluster components still represent the same phenomena but their membership or relations in the cluster are altered, there is currently nothing in prevailing philosophy of science accounts based on theories of reference that allow us to describe this variation in explanatory role. *Prima facie*, variation in the explanatory role of concepts in the midst of stable reference is something that the philosopher of science, whose goal it is to understand how scientific practice operates, does not want to ignore. This may also hold more generally for *meaning*.[24]

Third, the identification of particular patterns of difference or change in conceptual clusters, regardless of any differences in reference (or stronger, meaning) of constituent concepts, may be suggestive of interesting dynamics occurring in the practice of offering

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[23] For example, from an inferential role semantics account (e.g. Brandom 1994), every concept gains it *meaning* in a complex set of inferential relations with other concepts. Therefore, changes in conceptual clusters would imply changes in the meaning of concepts in the cluster.

[24] For example, if we think of meaning in Fregean terms as composed of two components, *sense* and *reference*, then if reference is stable and sense is understood in terms of conceptual roles (another assumption), it is not clear that alterations in conceptual clusters require alterations in conceptual roles thereby leading to a semantic difference. There appears to be a real possibility of variation in conceptual clusters that does not have semantic import.

explanations, especially concerning what factors may be *causing* the changes (evidential, sociological, or something else). There are questions about conceptual use that can be dealt with apart from concerns about reference. Differences in conceptual clusters can correlate with attention to different problems or differences in the standards for evaluating explanations between different disciplines. Understanding the nature of these differences directly addresses issues of when explanations are compatible or competing (Mitchell 1992; Sterelny 2001 [1996]), which is critical for evaluating claims about explanations of evolutionary innovations and novelties in the context of Evo-devo (understood as a disciplinary synthesis). Therefore, even if the account of conceptual clusters is detached from an explicit semantic interpretation, it can still serve as an eminently useful tool in dissecting the scientific activity of generating explanations.

Although conceptual clusters are offered by both individuals and groups of scientists in different contexts, socially articulated conceptual clusters (as found in presentations of explanations in journal articles) tend to be representative because they are shaped by disciplinary expectations (e.g. peer review) about which concepts are related to one another with respect to particular problem domains. Alterations on a more than individual or 'microscale' of analysis, the one most favored by many contemporary historians of science, can be identified. Another advantage concerns interpretations of conceptual confusion or difficulties in identifying a univalent conceptualization of phenomena. These tensions in scientific concepts that often follow the introduction of new evidence can be understood not as fragmentation into multiple concepts but as alterations in the conceptual clusters related to an explanatory target concept. There can be one concept but many different contexts, which are isolated differently by distinct problem agendas. This permits a circumnavigation of difficulties associated with a repeated invocation of particular concepts changing. A final, related gain is that this unit of analysis encompasses multiple concepts operating conjointly without raising unwieldy issues about conceptual schemes or frameworks (Burian 1979; Davidson 1984), whatever these may be.

1.3. Conceptual Differences Across Time: A Phylogenetic Approach to Philosophy of Science

Our explication of conceptual clusters has thus far been motivated by the philosophical questions outlined in the introductory section regarding disciplinary syntheses. Do explanations from different participating disciplines of Evo-devo have discernable conceptual differences? Are these differences required for an adequate explanation of evolutionary innovations and novelties? But we also identified related historical questions that emerge from the claims made by proponents of Evo-devo concerning innovation and novelty. These include whether the origin of evolutionary innovations and novelties was ignored or marginalized by mainstream evolutionary biology and whether during this historical period of time there were any relevant disciplinary differences. The purpose of this section is to argue that a historical approach is critical to particular kinds of philosophical analyses and sets out the historiographic perspective adopted in the execution of this investigation. Answers to the philosophical questions that motivated the tool of conceptual clusters are illuminated by answers to the historical questions and conceptual clusters can be deployed in producing these answers.

1.3.1. Historiographic Issues and Philosophical Method

Observing that conceptual clusters can exhibit periods of stability (equilibrium states) or change established a bridge to the historical dimension of analyzing conceptual differences and yielded a different way of identifying ‘conceptual change’ in science. Attention to conceptual *change* (or, more generally, scientific change) directs us to the role of history of science in executing philosophy of science research. During the 1970s a raging debate existed about the relationship between history of science and philosophy of science, specifically whether each required input from the other (Burian 1977; Giere 1973; Laudan 1977, ch. 5; Losee 1987). No clear resolution was reached and researchers largely parted ways committed to different answers. In the meantime, philosophy of science experienced a specialization trend. Much current research focuses on specific problems in delimited areas of science rather than attempting to generate general accounts of scientific explanation, rationality, or theories. There is also a larger set of issues that come under the purview of philosophers of science in their attempt to explain how science operates. This heterogeneity of explanatory goals and domains of investigation among philosophers of science invites a reconsideration of the question, 'what role does the history of science play in philosophy of science research?'[25]

It cannot be the case that history is necessary for every kind of philosophical analysis of science. A recent overview of contemporary research makes little to no mention of history and yet reviews philosophy of science research, both general and specific (Clark and Hawley 2003b). But this leads to a question more germane to the present discussion: what can an ahistorical philosophy of science tell us about scientific *change*? Returning to the review of contemporary philosophy of science (Clark and Hawley 2003b), there is no discussion of scientific change, with most authors treating metaphysical, epistemological, and methodological issues in ongoing research from different domains.[26] Although ahistorical philosophy of science can clarify existing scientific discourse, identify metaphysical conceptions implicit in theorizing, identify

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[25] I ignore how philosophy of science bears on the history of science (Laudan 1990; Losee 1987; Richards 1993).

[26] History is only used to frame outstanding issues that are currently under discussion, not because the *explanandum* of interest is scientific change. The introductory remarks are revealing in this respect: "Can any general conclusions be drawn from this collection about the nature of philosophy of science today? As the following papers show, current philosophy of science includes analysis of the epistemic status of scientific beliefs and practices, investigation of foundational, often metaphysical, issues in the special sciences, especially theoretical physics, biology and mathematics, and, both particular and general methodological issues" (Clark and Hawley 2003a, 1).

biases in particular methodologies, or offer formal principles based on idealized assumptions about how belief revision takes place, it cannot address the issue of epistemic change in science without some attention to history, however recent (Kuhn 2000 [1992]; Larvor 2000; Losee 1987; Richards 1993; Shapere 1984a). Formal accounts of belief revision (e.g. Bayesian) may be *partly* helpful in understanding conceptual change, but they cannot achieve this in isolation.[27] And even if they can be shown to apply in certain domains of science, this is not sufficient for extrapolation to all areas of science, let alone the history of science. Specialization within philosophy of science partly explains why the debate about the role of history of science in philosophical analyses of science no longer exists; few philosophical researchers are tackling how scientific change occurs because there are a host of other issues to occupy their attention. This suggests a natural, complementary division of labor, where different core questions in philosophy of science require different methodological strategies, but it also implies that a purely ahistorical philosophy of science cannot, in principle, answer certain questions in philosophy of science.

That historical studies of science are needed to answer particular philosophy of science questions, such as the nature of 'conceptual change', does not dictate how historical investigations will be used. There is almost universal disapproval of using the history of science as a database from which to confirm pet theories in philosophy of science, especially because these philosophical theories often end up structuring the historical investigation (Hacking 2002a, 51-72; Kuhn 1977b; Larvor 2000; Losee 1987; Maull 1976; Richards 1993; Shapere 1984a). Additionally, there is the danger of anachronism, interpreting the past in terms of present ways of

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[27] The problem is a 'reverse naturalistic fallacy' (*from* ought *to* is rather than *from* is *to* ought). Even if belief revision *should* or *could* take place in the manner described, there remains an open question whether scientists actually *do* revise their beliefs this way. Assessing this concern is not trivial as the calculi used derive from highly idealized and abstract belief revision principles, which demands substantive interpretive work to demonstrate their relevance to actual scientific practice.

thinking. But there is at least one *via media* that does not use history as confirmation nor necessarily fall into Whiggish narratives. Exploring the history of science because of foundational issues arising in contemporary scientific practice can be understood as a form of problem solving or a ‘satisficing’ strategy (Nickles 1985; Simon 1977 [1967], 1977 [1972]).

The main goal of problem solving is not confirming a theory or hypothesis of scientific change or establishing its generality using case studies (cf. Laudan *et al.* 1986; Laudan *et al.* 1992 [1988], Kuhn 1977b) but rather solving the salient problem in focus (cf. Suppes 1990). This transforms the issue of how history bears on philosophy of science evidentially because the goal is not first and foremost a general picture of the operation of scientific activity. Instead problem solving heuristics are generated to frame and advance our understanding of particular problem domains (Nickles 1985; Wimsatt 1980a).[28] The use of history does not commit the investigator to generating *the* history of a scientific domain, and even allows for *other* histories of the same domain to be recovered using different heuristic principles or tools. These principles or tools can be secondarily evaluated for applicability to other scientific domains.[29] It simultaneously allows closer attention to details and relevant context because the aim is not an overarching abstract theory of scientific epistemology applicable to all domains past and present (cf. Rasmussen 2001), and provides a more direct path to the normative import of philosophical research (Nickles 1985). Counterexamples are not ‘silver bullets’ of disconfirmation, one of the main complaints about attempts to build a general theory of scientific change from historical examples (Larvor 2000; Nickles 1985; Thagard 1988, ch. 7; Vicedo 1993).

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[28] “The satisficer does not adopt the goal of finding the perfect, or best possible, solution to the problem at hand. The satisficer only seeks a solution good enough to proceed to the next stage” (Nickles 1985, 259).

[29] “Although a single case study (or a few) cannot tell us which methodological principle or strategy is optimal for all of science, it can in principle inform us that a strategic move was good enough to handle a specific sort of problem” (Nickles 1985, 260). Simon gives a formal measure of the applicability of a heuristic across problems solving domains in terms of ‘heuristic power’ (Simon, 1977 [1967], 170-173).

But there is more at stake than generality and how the details are utilized; particular approaches to history yield different *kinds* of details, especially with respect to features of scientific change. Richards has given a helpful typology of models of historiography that charts some available options (Richards 1987, 559-593).

- ***Static***: scientific knowledge consists of a closed system that is transmitted intact through history
- ***Growth***: scientific knowledge steadily grows and accumulates through history
- ***Revolutionary***: scientific knowledge often requires a major upheaval during its history where the major forms of thought are dramatically altered (e.g. from ancient to modern in the 'scientific revolution')
- ***Gestalt***: scientific knowledge can routinely undergo major shifts in thought forms that generate fundamentally distinct ways of viewing the world, none of which are especially privileged (as in a gestalt psychology 'switch' when viewing a Necker Cube)
- ***Social/Psychological***: scientific knowledge is a function of social and/or psychological factors. This comes in two flavors: weak (influences scientific knowledge) and strong (determines scientific knowledge)
- ***Evolutionary***: scientific knowledge is the outcome of some type of selection processes on analogy with Darwinian evolutionary theory

The first three are largely ignored nowadays, while gestalt and especially social/psychological historiographies are favored among many historians of science. Richards prefers an evolutionary model that draws an explicit analogy with natural selection mechanisms operating on the 'conceptual systems' of scientists (Richards 1977, 1987). This preference is shared by many philosophers of science (and biology in particular) interested in documenting and explaining scientific change using some form of evolutionary epistemology (Bradie 1986, 1989, 2001; Campbell 1974; Hull 1988b; Hussey 1999; Plotkin 1987; cf. Thagard 1988, ch. 6). There are a variety of issues that attend these kinds of analyses but instead of criticizing any particular proposal I want to make a straightforward observation. There seems to be space for an evolutionary model of historiography that is not explicitly based on selection mechanisms. We can hold that scientific knowledge exhibits evolutionary change in the sense of 'descent with modification' without committing to a particular mechanism (such as natural selection) for the modification. The goal of this model would be to first reconstruct the patterns of 'conceptual' descent with modification before attempting to offer mechanisms (let alone general ones) for observed 'change'. In biological parlance, the goal is to construct a phylogeny, a phylogeny of epistemic units in science such as concepts or conceptual clusters.

1.3.2. The Phylogenetic Approach to Philosophy of Science

A 'phylogenetic' evolutionary model of historiography as applied to philosophical questions about science documents patterns of stasis and change for particular epistemic units with respect to foundational problems in scientific research on analogy with phylogenetic studies of species relationships.[30] This methodological strategy has been termed a 'phylogenetic approach to philosophy of science' (Lennox 2001c). The approach advocates the importance of historical trajectories for understanding foundational problems in contemporary science, which are often the locus of questions about scientific change, through an exploration of the *origins* of these problems, aiming to identify focal points where particular conceptualizations may have led to present difficulties (cf. Shapere 1984a). For the present study the foundational problem concerns whether or not current evolutionary theory is in a position to explain the origin of

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[30] Thus a "phylogenetic approach" does not directly engage evolutionary epistemology, which is concerned with causal mechanisms (see citations above). Vicedo has previously drawn an analogy between historical philosophy of science and systematics (Vicedo 1993), though the position is not elaborated, and Toulmin represents a genealogical process of conceptual variation and change (Toulmin 1972, ch. 3), though the analogy is drawn to selection processes rather phylogenetic reconstruction.

innovations and novelties and the relevant historical juncture spans from the emergence of the Modern Synthesis (1930s/1940s) to contemporary criticisms of Evo-devo proponents about the inability of neo-Darwinism in this explanatory capacity.

The formulation of theoretical frameworks in science is contingent and subject to local influences of many different kinds. Foremost among these influences are empirical considerations, but they are by no means determinative, and they operate in conjunction with other factors. Alternative pathways were available in the early stages of now mature sciences, some of which were pursued while others were ignored. Often the clues to understanding contemporary foundational problems are found in those alternatives left by the wayside. The philosopher of science utilizes his or her knowledge of *and* distance from contemporary science in conjunction with the history of science to isolate the nature of these underlying issues.[31] Foundational problems are usually associated with one or more concepts central to ongoing scientific research and are often foci of scientific change. Thus, the framework of isolating and understanding conceptual clusters and their equilibrium states can be directly conjoined with the phylogenetic approach to philosophy of science.

Phylogenetic studies often serve as frameworks for exploring process questions about the evolutionary origin of characteristic features of species. Hypotheses about causal mechanisms that explain changes in conceptual clusters derived from discernable phylogenetic patterns allow for different possible explanatory factors such as competition, social institutions, evidential findings, or internal tensions in a theoretical framework. Therefore, there is no advance commitment to one or another of these features as operative at all times and in all places with

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[31] An important difference exists between the philosopher of science using history with the phylogenetic approach and the historian of science. For the former, the investigation looks *backward* into history to understand the present situation regarding foundational problems in particular sciences. For the latter, the investigation narrates a segment of history *forward* to better understand its dynamics in a particular historical context.

equal importance (a consequence of the satisficing strategy). Also, the reconstruction of patterns of variation in conceptual clusters will likely be more robust when executed on many closely related species or 'type specimens' (Hull 1988a, 1988b). Phylogenetic reconstructions of phylum level relationships without dense taxonomic sampling are subject to a variety of errors (Adoutte *et al.* 2000). Also, phylogenies are extremely sensitive to the types of characters used to establish relationships. The analogue of this for the phylogenetic approach to philosophy of science is that phylogenies using different units of analysis may recover different phylogenetic patterns. Comparing and contrasting these differing phylogenies can be an informative meta-analytical strategy for understanding epistemic change in science, just as it is for systematics (cf. Bull *et al.* 1993; Chippendale and Wiens 1994; de Queiroz, Donoghue and Kim 1995; Huelsenbeck, Bull and Cunningham 1996; Huelsenbeck *et al.* 1994; Patterson, Williams and Humphries 1993; Wiens 1998). In different terminology, the biases of different heuristics and tools can be recovered through a comparison of the different phylogenies of epistemic units generated, potentially offering a more robust picture of scientific change (cf. Mitchell 2002; Wimsatt 1987).

Although the phylogenetic approach to philosophy of science is procedurally agnostic about what has caused particular scientific changes, some causal assumptions are required (such as a genealogical connection among the units). But these should be kept as minimal as possible in the absence of direct evidence.[32] We have secured this minimal assumption for conceptual clusters by focusing on the presentations of explanations, which are historical entities instantiated in the scientific literature, part of the socially articulated structure of scientific communication, with relations to previous presentations in earlier scientific literature (Griesemer

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[32] "Th[e] less we need to know about the evolutionary process to make an inference about pattern the more confidence we can have in our conclusions" (Sober 1988, 11).

1984; Griesemer and Wimsatt 1989).[33] Metaphysically, we are identifying conceptual cluster variation and stability in theoretical abstractions rather than mental representations (cf. Gärdenfors 2000; Laurence and Margolis 1999). The identification of variation or stability in conceptual clusters reconstructed from scientific literature is not an artifact provided there is sufficient 'taxonomic sampling', as the analogy with phylogeny demands.

Therefore, the phylogenetic approach to philosophy of science in this study tracks epistemic changes over time by attending to variation and stability in conceptual clusters.[34] These conceptual clusters are isolated by problem agendas connected with key concepts associated with foundational explanatory problems in contemporary science and reconstructed from the presentations of explanations found in the scientific literature, where they are related by descent to previous explanation presentations. Historical patterns identified then serve as guides to establishing a process-based account of why stability or change is observed. The methodology can be outlined as follows. (i) A foundational problem is identified in a particular research area and carefully characterized. (ii) A concept (or several concepts) central to the scientific conceptualization of this problem is (are) chosen as the focal unit(s) for investigation. (iii) An analysis is undertaken of how conceptual clusters are used in explanations concerning the focal concept in contemporary research, in an attempt to discern a conceptual cluster and (if extant) an equilibrium state. (iv) Historical investigation over a selected period of time is executed with respect to the focal concept to discern any conceptual clusters and equilibrium states. (v) Results from (iii) and (iv) are compared to identify interesting similarities and differences, the latter yielding a preliminary account of conceptual change. (vi) Results from

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[33] The ancestor-descendant relationships for conceptual clusters can also be transmitted by different mechanisms, such as in mentor-student relationships. But even for other types of transmission, the scientific literature is often involved, such as when a mentor gives a student papers to read that are authored by the mentor (cf. Kuhn 1977a).

[34] Different epistemic units can be utilized with the phylogenetic approach advocated here.

(iii) are compared against the explanatory demands articulated in (i) to determine if the structure of the conceptual clusters utilized in the present are actually positioned to address the supposed problem under consideration. (vii) The identification of any mismatch between the explanatory aims derived from the nature of the problem agenda and the current conceptual structure of attempted explanations leads to specific proposals for redressing the mismatch.

1.3.3. Normative Import of Philosophical Analysis

The last procedural step may be controversial because it is prescriptive. In order to clarify my claim, three different interpretations of philosophical normativity for science can be usefully distinguished: (a) 'weak' prescription based on standards putatively accepted by particular communities of scientists, past or present (holding researchers to their own commitments); (b) 'moderate' prescription based on standards that putatively apply across disciplines, past and present, and/or operate within and between specific domains of inquiry (Burian 1993b); and, (c) 'strong' prescription based on standards that putatively apply to any domain of inquiry referred to as science, past or present. Strong normativity was what exercised the logical empiricist research program (and others, such as Popper) and came under heavy fire by historicist researchers such as Kuhn and Feyerabend (cf. Shapere 1984a; Suppes 1990). Weak normativity is acceptable to most historians of science because it is relative to particular communities at specific times. Much contemporary philosophy of the special sciences exhibits this form of normativity in the attempt to clarify scientific concepts and determine the degree to which theories or explanations are evidentially supported. The moderate form occupies an interesting middle ground because it is not necessarily relative to a particular historical period or disciplinary approach but does not claim to bear on all scientific practice.

Here it is useful to appropriate (with some modifications) Friedmans's proposal for a three-tiered system of scientific knowledge (Friedman 2002). The first tier is composed of explicit principles and concepts of ongoing scientific practice that are routinely subject to empirical verification procedures; the second consists of "constitutive a priori" principles that are the implicit rules for using the first tier material in the ongoing project of science, including shared identification of problems; the third level has "philosophical meta-paradigms" that allow for transitions and communication between incommensurable scientific paradigms (not sharing second tier commitments). The moderate form of normativity I am advocating operates in an area similar to the second of Friedman's tiers. A foundational problem that exercises scientists across different research traditions exhibits a coordinating effect when a conceptualization is agreed upon and relevant conceptual differences are isolated among putative explanations.[35] But since problem agendas can differ radically across domains of natural phenomena, these kinds of normative recommendations will not necessarily bear on all areas of science or scientific research prosecuted at earlier times (cf. Losee 1987, ch. 6).[36] At the same time, the clarification of problem agendas will involve articulating their relations to other problem agendas and thus the normative recommendations will ramify beyond the immediate disciplinary contexts of the foundational problem under consideration. Demonstrations of conceptual cluster variation due to differences in the conceptualization of the foundational problem, whether between past and present or across present usages in different disciplines, serve as a forum for making research recommendations via shared criteria of adequacy for explanations of particular natural phenomena. This conception of normativity is not captured in critical discussions of prescriptive

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[35] Burian identifies a cognate notion of unification and coherence as 'middle range norms' (Burian 1993b), referring to the need for scientists to reconcile recognizably competing claims about a common subject matter.

[36] I do not mean to imply that the three forms of normativity *directly* map onto Friedman's three tiers, although there is a correlation that makes the comparison fruitful to illustrate the nature of moderate normativity.

philosophy of science because it does not focus on methods or theories, nor does it seek to generalize from a particular case study, as the satisficing method is based on research heuristics rather than exclusive claims about how scientists reason (cf. Kuhn 1977b; Thagard 1988, ch. 7).

1.4. Situating the Argument: Concepts, Conceptual Change, and Historical Epistemology

Now that we have developed the analytic tool of conceptual clusters and articulated the phylogenetic approach to philosophy of science, it is necessary to situate my account of conceptual clusters and their historical development in broader discussions of concepts and conceptual change. The goal of this section is to make appropriate contact with these disparate literatures to illuminate how an epistemological project focused on a specific situation in biology bears relations to other philosophical research. It also augments the original rationale for developing the tool of conceptual clusters, as well as that of problem agendas.

1.4.1. Theories of Concepts

Articulating a theory of concepts is an old problem for philosophers and a hot area of research for contemporary cognitive scientists and psychologists. There is widespread agreement that concepts are fundamental to human cognition, if not the fundamental units themselves,[37] but explanations of their nature quickly diverge. A variety of distinct theoretical positions can be recognized. A recent survey (Prinz 2002) identifies *definitionism* (concepts as full descriptions of necessary and sufficient conditions for something to fall under the concept), *imagism* (concepts as based on immediate impressions of perceptual information that can be secondarily associated), *prototype theory* (concepts as lists of salient properties permitting

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[37] E.g., "Concepts are the most fundamental constructs in theories of mind" (Laurence and Margolis 1999, 3).

categorization but the representation does not have to contain all of the properties of things that fall under the concept), *exemplar theory* (concepts as constituted by particulars that exemplify referents of the concept without requiring a set of shared properties), *informational atomism* (concepts lack internal structure), and the *'theory theory'* (concepts as ongoing explanatory projects or theories, subject to continual review and revision through interaction with the world), although other distinctions can be made (cf. Murphy 2002; Smith and Medin 1981).

Despite dramatic differences in these accounts of the nature of concepts, a key thematic strand emphasizing representation can be extracted. Psychologists have been primarily interested in the representational nature of concepts (how is conceptual content organized in the brain?) while philosophers' interest in representation has focused on how concepts refer. Considered together, the aim is characterizing the nature of mental representations and their referential functions. Motivation for this derives in part from an interest in how perceptual concepts are combined into more complex concepts and the experimental assessment of categorization phenomena (Solomon, Medin and Lynch 1999). Medin and Smith distinguish the taxonomic functions of concepts (categorization and conceptual combination) and expressing relations within the taxonomy (constructing propositional representations and interrogating propositional representations) (Smith and Medin 1981, ch. 2). This latter subcomponent of expressing relations, which concerns drawing inferences between and among concepts, is one that has received less attention (Solomon, Medin and Lynch 1999). A variety of philosophers have tried to understand concepts (and content) via a methodological commitment to their use or role in reasoning processes (e.g. Block 1986, 1998; Brandom 1994, 2000; Harman 1973; Horwich 1998; Peacocke 1992).[38] One feature exhibited in many of these analyses is an

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[38] This methodology is observable in variable forms in the work of earlier philosophers such as Frege, Wittgenstein, and Sellars (e.g. Sellars 1953, 1963 [1954], 1974).

emphasis on logical concepts, such as CONJUNCTION or ENTAILMENT. Both methodologies analyze basic concepts, whether perceptual or logical, and then move to other basic concepts (e.g. *from* logical *to* perceptual), and, in some cases, to more complex conceptual phenomena.

This distinction between two basic methodological commitments (representation or structure *versus* use or reasoning role) adopted by philosophers focused on concepts has been highlighted through a series of dichotomies (Brandom 2000, 2-22).[39] Most poignant to the present analysis concerns the basic methodological outlook articulated in Section 1.2.1: is concept *use* to be understood with a prior notion of *content* or should a notion of *content* be derived from attention to the linguistic *use* of concepts? Conceptual clusters are forged out of attention to how concepts are used in scientific explanations and (for the present study) we have remained noncommittal about implications for conceptual content. Language possession seems to be critical for scientific concept possession, even if it is not a prerequisite in other areas of thought (cf. Prinz 2002; Varley 2002). Because scientific concepts are linguistically anchored, analyses beginning with conceptual *use* or behavior may be insightful on their own without resorting to assumptions regarding a theory of content.

A second dichotomy is pertinent for contextualizing the present development of the conceptual cluster notion: is the meaning of a particular concept intelligible apart from other concepts ('atomism') or are multiple concepts involved in grasping the meaning of a particular concept ('molecularism')? Although the phenomenon we have explicated as conceptual clusters does draw attention to the joint behavior of concepts, conceptual clusters as such do not favor one or the other of these *semantic* theses. One reason for this seeming molecularism may be a consequence of the limited scope of the present study. Most philosophers take as a desideratum

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[39] Arguably, these different methodologies may be mutually enlightening. "The idea is to show what kind of understanding and explanatory power one gets from talking this way, rather than to argue that one is somehow rationally obliged to talk this way" (Brandom 1994, xii).

on their theory of concepts that it be applicable to all concepts (Prinz 2002, ch. 1). This investigation concentrates on scientific (or theoretical) concepts, which may bias the observations of conceptual use toward molecularism because the complex nature of scientific concepts appear unintelligible apart from other concepts (cf. Papineau 1996).[40] Empirical investigations have given credence to a continuum of conceptual connectivity, with some concepts being more isolated and others being more related to one another (Goldstone 1996).[41] It seems less plausible that concepts such as GENE or NATURAL SELECTION have their semantic value independent of other concepts. Most, if not all, scientific concepts have been built up out of sophisticated processes of abstraction and composition by communities of scientists over long periods of time (cf. Kelley 1984; Margolis 1999 [1996]).

One final reason why molecularism of conceptual behavior may not have received as much direct attention is worth noting. It emerges from the domain of analyzing biases in research heuristics or problem solving strategies used to explain different phenomena (Kline 1995; Simon 1977 [1967]; Wimsatt 1980a). Reductionist research heuristics start with a necessary, pragmatic division of a system under scrutiny from its environment and then add that the behavior of interest in this system is a consequence of its parts (Wimsatt 1980a). These two commitments lead to a third tactic, which involves executing any necessary idealization on the environment first rather than the system. In analyses of concepts, we can translate the use of this

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[40] The 'molecularism' of theoretical concepts has been recognized by philosophers interested in conceptual content: "in a wide range of cases a set of concepts has the property that one can give an account of possession of any one of its members only by mentioning what is involved in possession of the other members of the set. In such cases we have a local holism [molecularism]. … Where mastery of a concept requires grasp of a certain theory or type of theory, that fact will be incorporated in the possession condition. The point applies equally to a family of concepts that form a local holism. In fact, a common explanation of the existence of a local holism is that the concepts therein can be grasped only by their role in a certain kind of theory that contains all the other concepts in the family too" (Peacocke 1992, 10, 12; cf. Millikan 1984, ch. 19, 2000, ch. 7).

[41] Although it was not tested, Goldstone hypothesizes that abstract concepts may be more systematically interdependent than perceptual object concepts. Some psychological studies of concepts have been criticized for having an implicit commitment to molecularism rather than having discovered it empirically (Margolis 1995).

heuristic as the decision to divide one concept from its environment or context of other concepts (such as in a conceptual cluster), locate the activity of interest in the parts of the concept (or its perceptual basis), and proceed with a simplified (or no) account of the conceptual environment.

A reductionist research heuristic leads to distinct *biases* in model building, the design of experiments, and observations. For model building, a preference is given to explanations that appeal to intrasystemic properties rather than intersystemic ones (i.e. that involve the 'environment'). Generalization or elaboration by making models less simple or idealized is executed on the internal (system) structure rather than external (environment) structure. For experimental design and observation, observations of environment will be neglected compared with observations of the system, thus missing potential patterns of interaction. Related to this, environmental variables are kept constant during experimental manipulation, thereby hampering the possibility of identifying dependencies that system variables exhibit with environment variables. A model or theory is often deemed adequate under artificial or laboratory conditions without appropriate testing in natural environments, thereby potentially ignoring the significance of environmental variables.

These reductionist research heuristic biases are in many current philosophical analyses of concepts. Theories of concepts tend to explain the behavior of concepts (including reference) in terms of their internal structure, composition, or perceptual bases rather than their environmental correlates. They add details to descriptions of the internal structure or perceptual basis rather than adding complexity to the environmental structure. Observationally, interactions between a concept and its environmental constituents will be neglected (held constant) and therefore prevent the identification of any significant interactions. Thus models may not be robustly tested against variation in the context of a concept (cf. Gärdenfors 2000; Koslowski 1996; Koslowski and Thompson 2002; Solomon, Medin and Lynch 1999). Using the tool of conceptual clusters corrects for reductionist research heuristic biases as applied to conceptual use.[42]

1.4.2. The Problem of Conceptual Change

Conceptual 'change' or revision is a core issue in philosophy of science research. "Scientific cultures develop and change. …In short, the ways in which we interact with our physical environment, and the ways in which we think about it, have changed and will continue to change. But how is such change to be understood?" (McGuire 1992). And yet 'conceptual change' is an ambiguous phrase.[43] A variety of phenomena are referred to as conceptual change, including (cf. Burian 1987; Buzaglo 2002; Carey 1999 [1991]; Chen and Barker 2000; Ferrari and Elik 2003; Körner 1973; Lennox 2002; Nersessian 2002; Thagard 1992):

- introduction of a new concept (GENE)
- rejection or replacement of a concept (OSCULANT GROUPS)
- reclassification of things originally considered to fall under a concept (ASCIDIANS from MOLLUSK to CHORDATE), also interpretable as a change in the hierarchical relationship among concepts (from ASCIDIAN under MOLLUSK to ASCIDIAN under CHORDATE)

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[42] Wimsatt (and Griesemer) have also applied these considerations to the issue of conceptual change in science (Griesemer and Wimsatt 1989), but understand the 'environment' of concepts in terms of 'background assumptions' related to agreement about the nature of a problem, which allows the proposing of different answers to this problem. "Fixing the conceptual environment is therefore following a reductionist research strategy as described by Wimsatt (1980), but at the level of entire research projects rather than at the level of individual scientific problems" (81). On my account, the fixing of a problem does not fix the conceptual cluster but rather allows it to be isolated. Variations in conceptual clusters utilized in explanations of problem agenda phenomena can then be further scrutinized.

[43] "Conceptual change in science has been a "hot" topic for more than two decades. Yet, in spite of the strenuous efforts of a good number of philosophers and historians, our understanding of conceptual change is very poor. In spite of general acknowledgment of the importance of conceptual change, there is no general agreement about what it is, how it works, how it should be evaluated, or how far-reaching its consequences are. … there is no settled consensus concerning the nature or the workings of conceptual change. There is no generally accepted terminology in terms of which to describe concepts, systems of concepts, changes in concepts, or changes of conceptual frameworks. There is no agreement regarding the analytical tools appropriate to the examination of conceptual change, the criteria for individuating concepts or conceptual systems, or the means of separating "mere" change of belief of change of theory from conceptual change" (Burian 1987, 3). Keil makes a similar point in the MIT Encyclopedia of Cognitive Science: "But no one sense of conceptual change prevails, making it difficult to define conceptual change in uncontroversial terms" http://cognet.mit.edu/MITECS/Entry/keil2.

- sub-categorization: the partitioning of particular types within a concept (SELECTIVE versus DEVELOPMENTAL ENVIRONMENT)
- development of more abstract concepts (DEVELOPMENTAL RESOURCE for anything, including DNA, that can be inherited reliably and causally impact development)
- adding a new instance or set of entities as falling under a concept (discovery of a new species of butterfly; PORIFERANS are METAZOA)
- adding or deleting hierarchical relations among concepts (PLANARIANS express OTX GENES during BRAIN DEVELOPMENT, as do ARTHROPODS and CHORDATES [compositional]; particular Burgess Shale species [ANOMALOCARIS] are not ARTHROPODS [relational])
- refinement or expansion of 'defining' features of a concept (MAMMALS do not lay eggs *to* most MAMMALS do not lay eggs; only BIRDS have feathers *to* BIRDS and THEROPOD DINOSAURS have feather-type integuments)
- reorganizing relations among concepts (POPULATION STRUCTURE is an effect of EVOLUTIONARY CHANGE *to* POPULATION STRUCTURE is a cause of EVOLUTIONARY CHANGE)

The heterogeneity of these possible 'conceptual' changes calls into question whether or not there is a unified phenomenon of conceptual change to analyze and many philosophers of science have discussed scientific change or epistemic changes in science, emphasizing the 'change' component rather than it being 'conceptual' (Donovan et al. 1992 [1988]; Laudan *et al.* 1986; Laudan *et al.* 1992 [1988]; Solomon 1995). 'Scientific change' refers to any small or large adjustments over time in the epistemic frameworks or assumptions utilized by communities of scientists in their attempt to characterize and explain natural phenomena.

If we remain focused on 'conceptual change', philosophers of science have also largely concentrated their attention on the representational dimension of concepts, as in Nersessian's model-based reasoning account (Nersessian 2002, 2003) or Thagard's account of conceptual revolutions (Thagard 1992; cf. Thagard 1988, 1999; see also, Andersen and Nersessian 2000; Barker, Chen and Andersen 2003; Chen and Barker 2000; Gärdenfors 2000). Another primary concern has been how our concepts connect with the things they represent (reference), which arose out of the work of Kuhn and Feyerabend on the existence of incommensurability between scientific communities (Feyerabend 1981; Kuhn 1962; Sankey 1994). A prominent interpretation of incommensurability focused on the possibility of different meanings for the same terms used by competing paradigms or research traditions (*semantic* incommensurability). This was encouraged by descriptive theories of meaning and reference whereby terms obtain their meaning in a language community from a common set of descriptions ascribed to terms (cf. Devitt and Sterelny 1999). The interpretation seemed to imply radical theses about scientific change, such as any change in a theory will entail changes in the meaning of any term of the theory (Collier 1984; Davidson 1984; Sankey 1994; Shapere 1984 [1966]).[44]

An enduring response to semantic incommensurability claims was drawn from a causal theory of reference; the referent of a term is fixed by an initial ostensive naming event and continued reference to the *same* thing or stuff derives from a causal chain of use going back to the initial naming and/or continued reliable causal connection between the terms and the things represented (Devitt and Sterelny 1999; Donnellan 1966, 1970; Kripke 1980; Putnam 1973, 1975).[45] The discovery that what we call 'water' is composed of H_2O molecules does not imply that someone who did not have this in their description for the concept WATER is unable to communicate with someone who does. Two scientific paradigms can have different descriptions for a term and still be talking about the same thing (Devitt 1979). Some philosophers have taken these insights and developed accounts of conceptual change or progress in terms of an increase

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[44] Kuhn himself encouraged this interpretation in later writings: "Both Feyerabend and I wrote of the impossibility of defining the terms of one theory on the basis of the terms of the other. But he restricted incommensurability to language; I spoke also of differences in "methods, problem-field, and standards of solution" (Kuhn 1970, p. 103), something I would no longer do except to the considerable extent that the latter differences are necessary consequences of the language-learning process" (Kuhn 1983, 684).

[45] Even though stereotypical descriptions are used to pick out samples of kinds, these need not be applicable to all or most of the kind members. Scientists often pick out unobservable kinds through descriptions of their causal powers.

in the ways a term refers or has its referents fixed (Kitcher 1993), or by emphasizing the interplay of reference fixing and transmission with theoretical commitments (Kroon 1985), especially with respect to natural kinds (Boyd 1991, 1999; Griffiths 1997, 1999).[46]

Other interpretations of incommensurability have focused on the lack of a common measure between problems, data, or criteria of explanatory adequacy (Doppelt 1978; Sankey 1994, 1997; cf. Shapere 1984a). These interpretations seize on themes not addressed by the move to a causal theory of reference[47] and also connect directly with the epistemological issues that arise in the context of disciplinary syntheses such as how distinct research traditions with differences in core problems, methodology, research aims, and criteria of explanatory adequacy produce 'synthetic' or 'integrated' products. Shifting focus to reference left any existing meaning differences between communities of scientists unelucidated. It also did not offer insight into how scientists *resolve conflict* if they have different meanings for the same referent (assuming meaning is more than just reference); even if we can be confident of the transtheoretic identity of terms and their referents, questions remain about adjudicating theoretical differences that put research traditions into conflict (Brigandt in preparation-b; Collier 1984; Hacking 1983; Kuhn 1983; LaPorte 2004; Shapere 1984a).

The heterogeneity of 'conceptual change' identified highlights that there is more to the conceptual practices of scientists than reference and the epistemic dynamics of disciplinary syntheses in contemporary science raise similar issues to non-semantic incommensurability interpretations of historical episodes. The tool of conceptual clusters is designed to isolate conceptual differences relevant to these concerns. The phenomenology of the 'molecularism' of

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[46] Another reason for the lasting focus on reference is its connection to other thorny philosophy of science problems, such as debates about scientific realism (Andersen 2001; Boyd 2002; Smith 1981).

[47] Causal theories of reference have their own difficulties, as do hybrid theories attempting to recoup resources from descriptive theories (Brigandt in preparation-a; Devitt and Sterelny 1999; LaPorte 2004; Soames 2002).

conceptual behavior motivates an approach to the study of conceptual change that attends to their joint deployment: "… concepts, whatever they are, seem to have the property of being tightly connected to one another as they travel along trajectories of conceptual change" (Keil and Wilson 2000, 316).[48] Similarly, issues regarding erotetic incommensurability, which can lead to differences in criteria of explanatory adequacy (Doppelt 1978), also provide a further rationale for the development of the idea of a problem agenda. Both conceptual clusters and problem agendas serve as analytic tools that deal with epistemological issues surrounding conceptual change that conjointly attend disciplinary syntheses and non-semantic interpretations of incommensurability.[49]

1.4.3. Historical Epistemology

There is one other area of philosophical investigation to which our methodology and account of conceptual clusters needs to be related—the 'school' of analysis referred to as 'philosophy of the concept', exhibited in different forms by Bachelard, Canguilhem, and Foucault (Gutting 1989, ch. 1; 2001, 227-235). Canguilhem distinguished between the conceptualization of phenomena and the theoretical interpretation or explanation of these phenomena; particular conceptualizations (or concepts) can survive severe transformations of the theory interpreting and utilizing them. "A concept provides us with the initial understanding of a

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[48] Coordinate conceptual change has been used as a criticism of 'history of ideas' approaches that trace isolated concepts: "such an approach tends to ignore the fact that ideas are interrelated and interconnected. If we want to understand what someone means by an idea, we must see how he uses it, how it functions for him in a broader framework of convictions about the world. … ideas change and evolve. … Such changes can only be explained by looking at the shifting position of an idea within a broader conceptual network which is undergoing continuous modification. … to explain the changes wrought on a particular and specific concept, we generally must look to a larger unit than the concept itself" (Laudan 1977, 181). Laudan then advocates entire research traditions as appropriate 'larger' units as opposed to 'slightly larger' units such as conceptual clusters.

[49] Kuhn's relevance to disciplinary syntheses emerges in his clarification of paradigms as either disciplinary matrices or exemplars (Kuhn 1977a). But Kuhn aimed to characterize what was common to a particular scientific community whereas our aim has been to characterize a within discipline explanatory strategy (conceptual clusters) in the context of a problem shared across disciplines (problem agendas). By implication, the latter is not necessarily constitutive of any particular discipline (or paradigm).

phenomenon that allows us to formulate in a scientifically useful way the question of how to explain it" (Gutting 1990, 138). Concepts can thus be shared between rival theories and refer to the same phenomena while providing for distinct disagreements in how to explain the phenomena so conceptualized. This ability of concepts to operate in different theoretical domains was termed 'theoretical polyvalence' (Gutting 1989, 32ff; 1990, 138).[50] One can identify theoretical changes through a historical analysis of a particular concept even if the concept itself did not change its sense or reference. Canguilhem concentrated on the original formulation or appearance of concepts, such as the concept of REFLEX (Delaporte 1994, 179ff), but foundational problems surrounding concepts are a parallel point of departure (in the sense described for the phylogenetic approach to philosophy of science). For Canguilhem, this meant that 'scientific revolutions' are less common than sometimes thought and a historical analysis of conceptual change could be executed on periods of science not exhibiting severe epistemic ruptures.[51] In agreement with our contrast of conceptual clusters with Thagard's 'system of concepts' (Section 1.2.4), Canguilhem's perspective implies that analyses of conceptual change can and should be able to capture more subtle alterations in concept use not earmarked by the appearance of so-called revolutions.

Canguilhem also informs another issue we need to face: the challenge of anachronism. He was acutely aware of the difference between the history of a scientific term, e.g. 'mass' or 'gene', and the history of a scientific concept, taken as an understanding or conceptualization of some natural phenomena: "the historian should not make the error of thinking that persistent use

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[50] "If a concept outlined or formulated in such a context is subsequently captured by a theory that uses it in a different context or with a different meaning, it does not follow that the concept as used in the original theory is nothing but a meaningless word. Some concepts, such as the reflection and refraction of light, are theoretically polyvalent, that is, capable of being incorporated into both particle theory and wave theory" (Delaporte 1994, 181).

[51] Canguilhem was not reacting to Kuhn but rather Bachelard who had articulated the notion of 'epistemological breaks' and 'epistemological obstacles', which, while distinct, have points in common with Kuhn's articulation of scientific revolutions and incommensurability (Gutting 1989, ch. 1; 1990, 133ff; 2001, 229-230; 2003).

of a particular term indicates an invariant underlying concept (Canguilhem 1988, 11; cf. Delaporte 1994, 32-3, 36-8, 49-52). Histories of terms inevitably lead to the search for precursors, which ultimately obliterates the epistemological significance of the history of science (Gutting 1989, 1990). An implication of these warnings is that similar terminology may be misleading when attempting to identify stable conceptions that play a role in delineating conceptual clusters, as well as the possibility that past components of conceptual clusters may have no contemporary analogues. In order for a diachronic analysis of conceptual clusters to be undertaken, attention must be paid to translating the problem agenda in order to secure a similar conceptualization of the natural phenomena in need of explanation. I tackle this issue explicitly in Chapter 4.

Other contemporary philosophers interested in the historical development of scientific knowledge influenced by these approaches (usually through the work of Foucault) include Arnold Davidson and Ian Hacking. Canguilhem's work can be described as an epistemological history of concepts (Canguilhem 1988, 1-23), where histories of 'conceptualizations of phenomena' are documented. Arnold Davidson develops a 'historical epistemology' from studies of sexuality and psychiatry, which focuses on the conditions of comprehensibility for sets of statements in a scientific discourse (Davidson, A. I. 2001). He stresses a feature of conceptual behavior that converges with our methodological strictures: "concepts are to be identified by the uses that are made of them, by the connections that govern their employment and that allow them to enter into what Foucault thought of as specific 'games of truth'" (181). Ian Hacking has labeled a similar methodology 'historical meta-epistemology' or 'historical ontology'.

> [It is] a certain way of doing the history and philosophy of, among other things, sciences. … it talks *about* very general or organizing concepts that we use today, and which have to do with knowledge, belief, opinion, objectivity, detachment, proof, probability,

> argument, reason rationality, evidence … [and] it is called historical because it takes for granted that concepts of knowledge (etc.) are not pure concepts that can be analysed by reflection on the human understanding, or on the timeless structure of logic and language (Hacking 1999, 53; cf. Hacking 2002a).

Most germane for the phylogenetic approach to philosophy of science is Hacking's willingness to also treat workaday theoretical concepts in science (such as PSYCHIC TRAUMA) in addition to the organizing ones, which derives from an interest in current areas of contention in science, i.e. foundational problems (cf. Hacking 1999, 65).[52] His methodology also focuses on conceptual use: "concepts have no constitution other than tradition and use … don't ask for the meaning, we say, ask for the uses past and present" (56, 70).[53]

The relevant points of contact between these historical approaches to epistemology and my methodology can be summarized along two lines. First, it is similar to Canguilhem's historical epistemology but executed with respect to the origin of foundational problems that attend core theoretical concepts using the heuristic tool of conceptual clusters, where the analogue of theoretical polyvalence is *disciplinary polyvalence* in the sense of the same conceptualization (or explanatory target concept) being used with different cluster members and relations. Second, the phylogenetic approach to philosophy of science can be seen as a variant of Hacking's historical meta-epistemology with a focus on theoretical concepts found centrally within particular disciplinary foci in scientific practice rather than 'organizing' concepts that

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[52] "It is important for the historical meta-epistemologist not to fixate on the grand organizing concepts, objectivity, or, to move from epistemology to ontology, ideas such as the self or being a person. The objects of attention should be lower down on a conceptual hierarchy, in terms of what is organized … it is an essential feature of our work that one does not fixate on the grand organizing concept, objectivity or being a person. There are plenty of unnoticed, and hence worth noticing, concepts" (Hacking 1999, 61, 67). Hacking uses 'empirical concept' rather than theoretical concept to describe these 'other' concepts (cf. footnote 3).

[53] This links up with Canguilhem's distinction between concepts and the terms used concerning them. "A concept … is to be understood in terms of the words that we use to express the concept, and the contexts in which we use those words. …A concept is no more than a word or words in the sites in which it is used. Once we have considered the sentences in which the word is used, and the acts performed by uttering the sentences, and the conditions of felicity or authority for uttering those sentences, and so on, we have exhausted what there is to be said about the concept. … Concepts and words are not identical. … Evidence for difference in concept is provided by difference in site: the word is used by different classes of people to do different things" (Hacking 2002a, 35).

transcend special science research. Strong resonance exists between Davidson and Hacking's emphasis on conceptual use and the methodological strategy adopted in elucidating conceptual clusters. The philosophical task undertaken here, using the phylogenetic approach to philosophy of science with conceptual clusters and problem agendas as analytic tools, is *epistemology* from a *historical* vantage point.

1.5. Summaries and the Road Ahead

It is now time to summarize the main thread of argument articulated in this chapter. We began with the identification of concepts and problems as natural units of scrutiny arising out of the claims propounded within Evo-devo *qua* disciplinary synthesis that explanations of innovation and novelty were a distinct domain of inquiry falling outside the scope of neo-Darwinian evolutionary theory. Adopting a methodology that focuses on the use of epistemic entities prior to characterizing their nature, we started with the observation that theoretical concepts that represent natural phenomena in need of explanation have conceptual *contexts* that can be identified in explanatory projects. These were termed *conceptual clusters*. Conceptual clusters were explicated using two metaphors: toolkits and neighborhoods. The toolkit metaphor allowed us to recognize that scientific disciplines have a variety of concept types available, both owned and borrowed, and that only a subset are used for tackling particular problems. The neighborhood metaphor was used to address this subset, the conceptual cluster. It highlights how a diversity of concept tokens bear structural relations to one another in scientific explanations, especially regarding their evidential support for causal relations relevant for explaining features of natural phenomena represented by the explanatory target concept (the *reason* for constructing the 'neighborhood'). Conceptual clusters are isolated from explanation presentations using problem agendas and, like neighborhoods, contain historical traces of these structural relations, as well as exhibiting periods of stasis and change (termed *equilibrium states*).

Having developed the idea of conceptual clusters, we turned to whether historical research is needed to address particular philosophy of science questions such as scientific change, which often are centered on foundational problems in the sciences. Instead of offering a general scientific epistemology, we took up a problem solving or satisficing strategy to the use of historical evidence and advocated an evolutionary model of historiography that was not exclusively committed to natural selection as the mechanism of epistemic change. This model, termed the phylogenetic approach to philosophy of science, was explicated on analogy with the phylogenetic reconstruction of species relationships in systematics. It aims to trace the origin of foundational problems in contemporary science and patterns of conceptual use, specifically the behavior of conceptual clusters, related to these problems. After detailing how this method yields a moderate form of normative import for scientific practice, we situated conceptual clusters and the phylogenetic approach to philosophy of science in other philosophical discussions. With respect to theories of concepts, we observed that a methodological commitment to analyses that start with use and move to representation was less common and 'molecularism' in scientific concept use may have gone previously unanalyzed due to biases inherent in reductionist research heuristics. With respect to the problem of conceptual change, the heterogeneity of phenomena referred to as conceptual change is not captured by discussions of reference in the context of semantic interpretations of incommensurability. The epistemological issues identified for disciplinary syntheses share key similarities with those discussed in non-semantic interpretations of incommensurability, which strengthens the significance of conceptual clusters and problem agendas as analytic tools. Finally, we noted interesting points of convergence with historical studies of epistemology (Canguilhem, Davidson, and Hacking) and the congruence of notions such as theoretical polyvalence with conceptual cluster behavior in disciplinary syntheses.

Returning to our procedural steps outlined for applying the phylogenetic approach to the philosophy of science, we can now sketch the structure of the entire dissertation. In this chapter we identified the foundational problem of explaining evolutionary innovations and novelties currently in the foreground of Evo-devo research and the characterization of this problem is undertaken in Chapter 2 alongside an explication of problem agendas. Chapter 3 illustrates problem agendas in the concrete area of the origin of avian feathers and flight. Because the concepts of EVOLUTIONARY INNOVATION and NOVELTY represent the natural phenomena central to the problem, they serve as natural foci for the investigation and, in part, motivated the development of the conceptual cluster tool. Investigations of different contemporary disciplines attempting to explain the origin of innovations and novelties are undertaken in Chapter 5. A parallel investigation for portions of the relevant historical period is executed in Chapter 4, with a special focus on three different researchers from key disciplinary contexts. In Chapter 6, the past and present conceptual clusters are reconstructed and the results are compared to identify interesting similarities and differences. Additionally, these explanations are evaluated against the criteria of explanatory adequacy elucidated for the problem agenda in Chapter 2 in order to determine if the structure of the conceptual clusters utilized in the present are positioned to address the problem under consideration. These comparisons yield particular mismatches between the predominant emphasis on developmental genetics in current Evo-devo methodology and criteria of explanatory adequacy elucidated, reiterating the genuine need for Evo-devo to be a disciplinary synthesis. Trends of 'molecularization' in biological disciplines, especially embryology, and their impact on conceptual use partly explain the origin of this mismatch (cf. Fraser and Harland 2000; Morange 1998).[54] The final chapter attempts to address the applicability of the methodology exhibited here for other domains of investigation in philosophy of science, to what degree we can consider it a *testable* thesis about conceptual behavior, and delineate related questions emerging out of the overall analysis offered.

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[54] Molecularization can be considered to include: (1) using the techniques of molecular biology, especially recombinant DNA technology but also physical and structural chemistry techniques; and, (2) using the evidence accumulated from these techniques to provide an independent route to undergird or overturn distinctive features (concepts, explanations, etc.) of a particular biological discipline. This description is from a paper by Bob Olby entitled, '"Memory Molecules": A Case Study in the Impact of Molecular Biology on the Neurosciences?' (2002).

2. THE PROBLEM AGENDA OF EVOLUTIONARY INNOVATION AND NOVELTY

2.1. Introduction: Problems in Focus and Individuation

In the previous chapter we identified both concepts and problems as natural units to concentrate upon when analyzing explanations of evolutionary innovations and novelties in the context of Evo-devo. The rationale for attention to problems derives from claims that innovations and novelties should be considered a distinct domain of inquiry.

> The notions of evolutionary innovation and particularly of evolutionary novelty make sense only if they support a distinct research program (Müller and Wagner 2003).
>
> The origination of morphological structures, body plans, and forms should be regarded as a problem distinct from that of the variation and diversification of such entities (the central theme of current neo-Darwinian theory) (Müller and Newman 2003b).

How are we to understand the claim that the origin of evolutionary innovations and novelties is a ‘distinct problem’? Biologists since before the time of Darwin have been struck with two aspects of living entities: their tremendous diversity and their exquisite adaptedness to environmental surroundings. These are the natural phenomena that demanded an explanation, posing a core domain of problems in the eyes of most biologists. In the 20th century, the most successful theoretical framework for dealing with the phenomena of adaptation and diversity was the Modern Synthesis (‘neo-Darwinism’), which emphasized natural selection operating on small effect mutations manifested as gradual phenotypic differences in local populations (Sterelny and

Griffiths 1999, 22-52). Despite strong claims that, “no phenomenon has ever been found in organic nature that cannot be interpreted within the framework of the modern, synthetic theory of evolution” (Mayr 1959), biological researchers have acknowledged the explanatory limits of natural selection: “Natural selection cannot explain the origin of new variants and adaptations, only their spread” (Endler 1986, 51). Although the issue of the origin of new variants has long been used as a criticism of the explanatory power of natural selection (Bowler 1988), here the origin of new variation is interesting because it begins to pick out what is distinctive about natural phenomena (such as bone, endothermy, feathers, flight, neural crest cells, tetrapod limb, turtle carapace, and vertebrate jaws) collected under the concepts EVOLUTIONARY INNOVATION and NOVELTY. But in addition to *distinguishing* the problem there is also a need to *characterize* what it consists in. The ability to distinguish innovation and novelty from domains of inquiry extant in evolutionary biology, such as adaptation, and characterize the explanatory burden associated with these phenomena is critical to evaluating the potential of Evo-devo to provide mechanistic explanations for evolutionary innovations and novelties that genuinely expand the ‘explanatory range’ of evolutionary theory (Wagner, Chiu and Laubichler 2000).

Before this endeavor is begun a more basic question rears its head: what exactly does it mean to talk about *distinct problems* in the biological sciences? In Chapter 1 we briefly met the notion of a *problem agenda*, which is the problem-related unit of analysis I will be developing to address these issues. Problem agendas served as the source of isolating conceptual clusters because they represented the targets of explanation. They were also motivated by other philosophical concerns arising from non-semantic interpretations of incommensurability (differing questions or problems, differing methodology, differing criteria of explanatory adequacy), which are directly relevant to the epistemological issues that attend disciplinary syntheses such as Evo-devo. Several independent reasons can be marshaled for focusing on problem-related units.

First, analyzing scientific problems highlights the goals or agenda of research. Making explicit the purposes of scientific disciplines is fundamental to comprehending their mechanical operation. Problems, questions, and research goals are the epistemic engine of scientific investigation and allow us explain *differences* in how or what is known. Concentrating on what exactly is being explained can illuminate the adoption of a particular style of reasoning or methodology. It also addresses the issue of two or more competing theoretical frameworks that attempt to explain the same natural phenomena, where reference is not at issue, and draws attention to recurring problems that get addressed but never fully answered within scientific research areas.[55]

Second, it offers clarification and rationale for both methodological choices and the standards adopted to judge the adequacy of explanations that concern the problem. Why scientists use a particular experimental technique or are unwilling to countenance specific kinds of explanations for certain natural phenomena are often motivated by a conception of what the underlying question concerns (whether well- or ill-formed). A basis for normative recommendations regarding methodological choices is purchased for a shared problem. If there is consensus on the nature of the problem (what it is and what its explanatory burden is), then there can also be recommendations that emerge from mismatches of current investigatory practice with the elucidated criteria of explanatory adequacy.

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[55] "Is it possible to discuss method intelligently unless the question of aim is first given thorough and serious consideration? Is not a method, by virtue of the very fact that it is a method, something which is subordinate to an aim and determined by that aim? Is not a method something which is to be understood, evaluated, attacked and defended only in relation to the particular aim which it serves?" (Somerville 1935, 246). "The recognition of a problem requiring a solution or a question deserving an answer is a step that must be taken in every sort of systematic study, and, therefore, that a problem is a more important characteristic of scientific method than a hypothesis" (Smith 1945, 296).

Third, problems illuminate disciplinary structures and their interaction (or lack thereof), one of the major issues bearing on Evo-devo and its claims concerning explanations of innovation and novelty. Cross-disciplinary interaction rarely occurs spontaneously and it is often driven by a commitment to a similar question, however independently arrived at (Bechtel 1986b, 1993; cf. Broido 1979; Klein 1996, ch. 2; Kockelmans 1979a). The articulation of criteria of explanatory adequacy serves to clarify existing scientific discourse, assess proposed solutions, and negotiate disciplinary interaction using the scientific problem as a template (or guide). Epistemological conflicts in methodology and criteria of explanatory adequacy observed in interdisciplinary endeavors can be adjudicated such that the relative contribution of each discipline to the common problem is recognized and defined.

Fourth, theoretical or methodological resources do not uniquely or exhaustively determine the conceptualization of natural phenomena and scientific problems. Although it is certainly true that the construal of scientific problems is affected by the resources or methodologies adopted to deal with them, the problems are not wholly dependent on these.[56] What scientists *want* to know is conditioned in part by what they already *think* they know but certain problems or targets of explanation persist (though in different guises) through alterations in scientific knowledge structures. In a different context Canguilhem refers to this persistence of conceptions of biological phenomena as 'thematic conservation'.[57] There can be a shared commitment across divergent theoretical frameworks to explain certain sets of phenomena and capturing this persistence is part of our methodological desiderata. If we can identify what kinds

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[56] Thus, I think it is only partly true that, "each [scientific] style introduced new objects of scientific inquiry and explanation, new types of evidence, and new criteria determining what counted as the solution of a problem. … each [scientific] style defined the questions to be put to its subject-matter and these yielded answers within that style" (Crombie 1994, 83, 85; cf. Davidson, A. I. 2001, 141).

[57] "For the alleged principle of thematic conservation in the history of biology is perhaps only a reflection of the biologist's acceptance in one way or another of the indisputable fact that life, whatever form it may take, involved self-preservation by means of self-regulation" (Delaporte 1994, 205).

of things remain across epistemic ruptures in theoretical frameworks, then there is a distinct basis for discerning the contours of *what* changes and *how* in the history of science. In sum, the four preceding reasons indicate that focusing attention on scientific problems (*not* the problem solving capacity of scientific theories or paradigms) is a highly favorable analytic strategy.

The structure of this chapter is as follows. Section 2.2 addresses the fundamental issue of what it means to talk about different scientific problems. There I articulate the notion of a *problem agenda*, which is an investigative unit for philosophy of science that clarifies what it means to talk about 'different' problems in biology (and other sciences). I draw on resources from Aristotle's discussion of problems (Lennox 2001a) and van Fraassen's pragmatic theory of explanation (van Fraassen 1980, ch. 5) to analogically explicate scientific problem agendas. This sets the stage for Section 2.3 where I distinguish and characterize the problem agenda of evolutionary innovation and novelty by using this philosophical analysis. In particular, I attend to three primary dimensions for the problem agenda: (1) the origin of functions versus forms; (2) the level of biological hierarchy in focus; and, (3) the generality of theoretical and experimental investigations of function and form at different levels. An elucidation of the detailed consequences of my analysis of the problem agenda of innovation and novelty, especially as it bears on contemporary Evo-devo research, is deferred until Chapter 6, although I draw out several immediate results. Section 2.4 situates my account of problem agendas in the existing philosophy of science literature on problems, highlighting similarities and relevant differences.

2.2. Problem Agendas

Problem agendas are units of investigation for philosophy of science referring to any distinguishable set of related phenomena that pose a suite of intertwined research questions.

These questions are investigated with the aim of providing a satisfactory theoretical framework capable of addressing all of the component phenomena. *Problem* highlights the emphasis on that which is unknown, uncertain, or perplexing – questions rather than answers. *Agenda* is used to subsume the multifaceted nature of the unit. What is unknown is not one thing, but many, a sort of 'list of things to be done' by a group of scientific researchers. These researchers address the problem agenda through the development of a satisfactory explanatory framework. Problem agendas are larger units of analysis than individual empirical or theoretical problems. Sets of problems related to a circumscribed set of natural phenomena are less likely to be fundamentally altered if one or another of the member problems is altered or adjusted.[58] Problem agendas can be thought of as the 'big' questions (abstractly framed) concerning a particular domain of inquiry. Most individual researchers focus their attention on more concrete *research questions* ('empirical problems') within the context of specific biological systems that are connected to one, or usually more than one, distinct problem agenda. These research questions are addressed theoretically or experimentally using a variety of different formal and laboratory techniques. Answering research questions contributes to a greater understanding of the problem agenda phenomena. Problem agendas are a combination of particular domains or objects of study with the cognitive activity of asking questions about these domains (cf. Bechtel 1986b).

Problem agendas, in the sense described, are of particular relevance to disciplinary syntheses. Because researchers are primarily focused on research questions in concrete biological systems that often overlap with the concerns of multiple problem agendas, it is possible for investigators from different disciplines to be working within the same problem agenda but asking different questions concerning it. A careful delineation of the problem agenda

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[58] This difference is critical for applying problem agendas historically. Problem agendas can be *stable* without being *static* (cf. Laudan 1977, ch. 6).

and its explanatory burden can illuminate to what degree these different disciplines are offering complementary answers to different questions or competing answers to the same question. It may also establish what kinds of conceptual resources are required to adequately explain the objects under scrutiny. This is especially important for evaluating the need for disciplinary syntheses. Only with a full articulation of the criteria of explanatory adequacy can there be a satisfactory assessment as to what disciplinary contributions, in principle, are required to address particular questions in the problem agenda.

A short example is helpful to illustrate the idea of a problem agenda. One enduring problem agenda in biology is that of *classification*—how are the millions of different 'species' on our planet related and on what principles (natural or artificial) can we (or should we) carry out a systematic enterprise? The research questions under this problem agenda usually pertain to discerning the appropriate classification for a group of organisms (arthropods, angiosperms, etc.) but also include questions about the appropriateness of particular methodological principles, such as parsimony. A variety of theoretical and experimental work can be done with different techniques to ascertain relevant morphological and molecular features that produce hypotheses concerning relationships within and between these groups. The final goal is to have a robust set of principles, procedures, and worked out cases in order to be convinced (as a scientific community at a particular time) that the problem agenda has been adequately addressed.

Other problem agendas include adaptation, organismal ontogeny, ecology, cellular division and differentiation, and inheritance, to name a few. One problem agenda can have close relations to another problem agenda and the nature of these relations is important for clarifying what is required for adequate explanations. A problem agenda can be both *temporally stable* across long periods of time through tremendous upheaval in the explanatory frameworks taken to satisfactorily address the problem agenda phenomena and *spatially stable* between competing explanatory frameworks. One of the main bases for this is referential stability of the phenomena across these different explanatory frameworks. The transitions between (and sometimes coexistence among) Aristotelian, Linnaean, idealistic, evolutionary, and phylogenetic systematics and their corresponding research questions, principles, techniques and available data are dramatically different but each is still concerned (at least in part) with the same problem agenda of classification with many of the *same* phenomena.

Our present question ('is there a distinct problem concerning innovation and novelty in biological research?'), as well as interconnections among problem agendas, leads us to ask how they will be individuated. We need a way to pick out why phenomena are 'related' and questions about them 'interrelated'. Some help can be drawn from an ancient discussion by Aristotle concerning the similarity and difference of problems in the *Posterior Analytics* (Lennox 2001a). In his discussion of 'scientific' problems, Aristotle worries about when we can say problems are the same and identify how they are different (*APo* II. 15 98a24-34). His answer (following the exegesis of Lennox), is: (1) certain problems are the same because they have the same middle, or, they are the same problem in kind, though different in form; and (2) certain problems, while related, are different because the middle which explains problem A *is* problem B, which is explained by another middle. Aristotle's example of related but different problems concerns increased Nile river flow at month's end. The first problem, 'why does increased Nile river flow occur at month's end?', is answered with, 'Because storms occur at month's end.' But this explanation begets a new problem that requires a different kind of answer. 'Why do storms occur at month's end?' – 'Because waning of the moon occurs at month's end'. Thus, Aristotle is able to distinguish these problems because the range of answers that could be supplied in response to the questions is qualitatively different.

This strategy requires agreement about the legitimacy of the questions. Disputes about whether there is increased Nile river flow or storms occurring at month's end need to be settled before distinguishing between the problems. This agreement concerns the role of theoretical resources and our current state of knowledge in understanding the structure of problem agendas. If a problem agenda is largely conditioned by current theories, then it will undergo drastic changes upon the abandonment or rejection of these theories and therefore be quite unstable across historical periods of time. A glance through the history of biology suffices to reveal that certain phenomena do persistently demand an explanation in the eyes of investigators from very different theoretical backgrounds. Aristotle was concerned to explain development and adaptation in ways quite recognizable to modern biologists (Gotthelf and Lennox 1987; Lennox 2001b). And yet certain phenomena originally considered separate can be brought together into a common domain (e.g. electricity and magnetism) and phenomena originally thought to demand one kind of explanation can be partitioned and dealt with using separate theories (e.g. quantum physical phenomena and cosmological physical phenomena). Problem 'collapse' and 'bifurcation' must be recognized (cf. Nickles 1976; Shapere 1977), as well as 'shifts' from one to another (cf. Lakatos 1970; Maull 1977).

Part of a solution relevant for the present discussion is to look for 'theoretical constraints' in the present that allow one problem agenda to be separated from another (cf. Nickles 1978). These constraints are often weak principles of consensus that are not in contention even between competing explanatory frameworks supposedly dealing with the same phenomena. If problem agendas can be distinguished using these, then the result should be acceptable among multiple scientific participants. The absence of these theoretical constraints in the past may have prevented a similar individuation of problem agendas, but it does not stop us from identifying that previous researchers were concerned with particular problem agendas we distinguish in the present. The weakest and most stable theoretical constraints are often (but not always) acknowledgments of what sets of phenomena need explanation, what I term *presuppositions*, though these alone may not be sufficient to *formally* distinguish problem agendas.

For a purely historical study, theoretical constraints could be identified that were applicable to the particular period under scrutiny. For example, we could ask on what basis Aristotle distinguished one scientific domain from another and assess the cogency of his executed separations without having to commit to that specific rationale today (cf. McKirahan 1978, 1992). The goals of this analysis are whether a problem agenda can be distinguished from another *in the present* given certain theoretical constraints and whether one can identify past researchers as having been focused on the concerns relevant to the problem agenda we are now able to distinguish (i.e. did they share the presupposition of acknowledging the need for an explanation of the problem agenda phenomena?). Distinguishing problem agendas involves a theoretical context, but this context need not have been present *in the past* to identify investigations as relevant to the problem agenda *in the present* (cf. Nickles 1976).

Thus far my introduction of the idea of scientific problem agendas has been informal, attempting to sketch main contours and give a rough conception of the perspective against the backdrop of earlier analyses. How might we make the notion more precise? One fruitful approach is to make analogical inferences using existing theory from philosophy of science. Since problem agendas are *epistemic* units as formulated, one potentially rich source to drawn upon is van Fraassen's pragmatic account of explanation that is formalized in terms of questions, answers, and the relations between them (van Fraassen 1980, ch. 5, esp. §4).[59] This discussion is especially relevant as it draws from Aristotle's writings on explanation, a source we have already tapped for problem individuation tools, as well as the formal logic of questions and answers (Belnap and Steel 1976), which explicitly foregrounds the role of making criteria of explanatory adequacy explicit.[60] van Fraassen argues that an explanation should be construed in terms of answers to why-questions, which demands a theory of why-questions.[61] Paraphrasing the elements elucidated by van Fraassen (labeled, vF), we can extract parallels for problem agendas.

- (vF) A *question* is an abstract entity expressed by an interrogative
    - A *problem agenda* is an abstract entity that is expressed by a suite of interrelated questions drawn from a domain of natural and/or experimental phenomena. The cohesiveness of the domain of phenomena and interrelations of the questions are a function of theoretical constraints.

- (vF) Basic typology of answers: *direct* and *indirect*, *partial* and *complete*
    - *Solutions* to a problem agenda can be considered partial or complete. A complete solution implies direct answers to all member questions.

- (vF) a *presupposition* of a question is any proposition that is implied by all direct answers to it
    - a *presupposition* of a problem agenda is a theoretical commitment to one or more of the phenomena under scrutiny

- (vF) a *corrective answer* is any denial of any presupposition of the question

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[59] This analogical exploring does not require that all objections raised against van Fraassen's account (such as the objectivity of the relevance relation) be addressed. I am not offering a *theory of* explanation.

[60] "For a query system and a user to agree on the meaning of a question is for there to be agreement as to what counts as an answer to the question, regardless of how, or if, any answer is produced" (Belnap and Steel 1976, 2). This does *not* mean that the contrast class of answers needs to be exhaustively specified in advance.

[61] van Fraassen's account synthetically blends the different sources indicated but I will not distinguish them here.

    - a *corrective solution* to a problem agenda is a denial of one or more of its presuppositions; i.e., that the phenomena under scrutiny are either not real *or* not distinct

- (vF) *complete answer* – relative to a theory, something that together with the theory implies some direct answer
    - relative to theoretical constraints, a scientific knowledge structure (theory, paradigm, etc.) *solves* a problem agenda by providing complete answers to each member question. Criteria for a genuine solution are dependent on the nature of and questions in the problem agenda.

Some of these analogical inferences remain closer to van Fraassen's original account while others depart into different territory. For example, instead of collecting a theoretical commitment to the phenomena and theoretical constraints under the idea of a presupposition, they are separated in order to allow a concentration upon differences that may exist between researchers over the acceptance of an explanatory demand pertaining to phenomena even though there is agreement with respect to theoretical constraints.[62] This pushes us to another disanalogy because answers are not relative to theories but relative to theoretical constraints, a move which aims to capture how two different theories might offer competing explanations of the same problem agenda phenomena with shared theoretical constraints.

In addition to these parallels, we can also mine van Fraassen's 'formalism' similarly to draw out more structural characteristics of problem agendas.

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[62] Most discussions of interrogative presuppositions explicitly link them with theories: "It is natural to think that these presuppositions are derived from theories. To the extent there are, say, Kuhnian disciplinary matrixes, there can be well-entrenched (and not always propositional) presuppositions which structure the why-questions of a given field; they mark out gaps in the available body of knowledge" (Sintonen 1984, 173; cf. van Fraassen 1980). Distinguishing presuppositions (as theoretical commitments to distinctive phenomena in need of explanation) from theoretical constraints allows for a larger space of possibilities that is relevant for understanding disciplinary syntheses such as Evo-devo (see Section 2.4, below).

- (vF) Why is it the case that P_k? P_k : *topic*, *explanandum* phenomenon
- Question as ordered triple: $Q = \langle P_k, X, R\rangle$, where X is the *contrast class* ($X = \{P_1, \ldots, P_k, \ldots\}$) and R is a *relevance relation* between *answer* A and $\langle P_k, X \rangle$. R related to contextual specification of questions.

- Why is it the case that $\phi_1, \phi_2, ..., \phi_n$? $\phi_{1, ..., n}$: *explanandum* phenomena
- Problem agenda as 'triple': *Problem Agenda* = $\langle \phi_{1, ..., n}, X, R\rangle$, where there is a set of *interrelated questions,* $X = \{Q_1, \ldots, Q_n\}$, and R = *relevance relation* between $\langle \phi_{1, \ldots, n}, X \rangle$ and *set of generalized answers,* $\{A_{1, \ldots, n}\}$. The problem agenda *relevance relation* is a function of the theoretical constraints that partly identifies the appropriate contrast class of generalized answers via individuation in conjunction with characterization.

Again, there are points at which these analogical moves are either closer or farther from van Fraassen's original intent but the goal is not to preserve his account but utilize it as a template. For example, van Fraassen requires a specified contrast class before a question is well defined while problem agendas maintain their integrity even if some interrelated questions are better specified than others. Because problem agendas are comprised of question sets related to a circumscribed set of natural phenomena, they are less subject to transformation during the process of clarification and adjustment pertaining to particular member questions.

Undoubtedly, there are other domains to probe analogically that would yield insights concerning how to construe problem agendas (e.g. Bromberger 1992; Hintikka 1981; Sintonen 1984). The notion of a problem agenda is intended to highlight *question groups* (that which is unknown) not methods or tools used to explain or answer. The existence of many problem agendas that have various interrelations earmarks the key issues that need to be attended to: individuation or the distinctness of problem agendas, and their careful characterization.

2.3. The Problem Agenda of Evolutionary Innovation and Novelty

2.3.1. Individuating the Problem Agenda

Because the phenomena of adaptation and diversity have been the central focus of much evolutionary theory and the Modern Synthesis emphasized the important causal role of natural selection in explaining these in terms of gene frequency alterations, it may be unsurprising that the standard way of tackling innovations and novelties was through a similar type of explanation. “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, 357). Can the origin of novelties be subsumed under a selection explanation used to address adaptation or is this intertwining problematic? One reason to be worried is that the ‘developmental’ gap between small gene mutations and structures having selective value can sometimes be quite large. Procedurally, there is an assumption about developmental processes that the relationship between genotype and phenotype is relatively straightforward. If it is not, then the developmental processes themselves will be required to explain the actual translation of gene mutations into new structures that could have selective value.

In his extended discussion of the structure of evolutionary theory, Gould isolates this as a critical node for assessing any need to revise evolutionary theory.

> Darwin insisted that his admittedly weak and negative force of natural selection could, nonetheless, under certain assumptions (later proved valid) about the nature of variation, act as the positive mechanism of evolutionary novelty–that is, could “create the fit” as well as eliminate the unfit–by slowly accumulating the positive effects of favorable variations through innumerable generations (Gould 2002, 14).

The key problem in Gould’s summary is the phrase “create the fit” because the claims about the nature of variation he is interested in challenging (copious, small in extent, and undirected) do not underwrite the assumption about developmental processes having a straightforward mapping of genotype to phenotype. That variation exhibits these three features does not create the fit, but rather explains how natural selection can create the fit. In order to create the fit, developmental processes have to generate variation in the first place. Whether straightforward or complex mappings between genotype and phenotype underlie copious, small in extent, and undirected variation (assuming their validity) has not been addressed. Returning to Endler's point, the fit is created by the *spread* of beneficial variants in the population, but natural selection itself does not explain the *origin* of variation (beneficial or not) that can be spread (cf. Endler 1986, 51). And this is important because neo-Darwinism has a theory of genetic level dynamics (population genetics) and a theory of phenotypic level dynamics (quantitative genetics) that are linked by developmental assumptions (cf. Ridley 2004).

The two problem domains, adaptation and novelty, can and should be pulled apart along lines of reasoning lurking in Gould's discussion and Endler's acknowledgment. The problem agenda of adaptation concerns the relationship between organism and environment, especially the tight fit that many organismal features appear to have with obvious and subtle aspects of their external surroundings. The *problem agenda of innovation and novelty* is concerned with explaining the origin of qualitatively new features in the history of life (e.g. neural crest cells, bone, body plans, jaws, feathers, and limbs). With the notion of a problem agenda explicated, we can begin to flesh out this claim in detail for these two putatively distinct domains of inquiry.

There are at least two basic reasons why the problem agenda of adaptation can be distinguished from that of innovation and novelty. The first is historical in that the problem agenda of adaptation was extant prior to the problem agenda of innovation and novelty. Investigators recognized the phenomena of adaptation as in need of explanation (a presupposition) prior to the recognition of phenomena referred to as evolutionary innovations and novelties. Ascertaining the intricate connection between organism and environment exercised 18th century British parsons (among many others) long before any evolutionary outlook had begun to emerge, and can be discerned among the scientific concerns of the ancient Greeks. The problem agenda of innovation and novelty (how vertebrate jaws or the tetrapod limb originated) does not exist without a genealogical understanding of the relationship between species over large spans of geological time via descent with modification. Thus, the problem agenda of evolutionary innovation and novelty required the introduction of a theoretical constraint, a historical perspective on species and their genealogical relations by descent with modification, before the investigators could recognize the phenomena as requiring explanation.[63] An important corollary of this, observable once a broadly evolutionary viewpoint achieved consensus, is that these two problem agendas have had different disciplinary 'homes'; adaptation was primarily the focus of natural history, population genetics, or ecology whereas innovation and novelty were the province of morphologists, paleontologists, and comparative embryologists (Love 2003a; Love and Raff 2003; Raff and Love 2004).[64] This difference in research focus for these biological disciplines reinforces that what unified the phenomena in need of explanation for adaptation and evolutionary innovation and novelty were not identical.

A theoretical commitment to the phenomena in need of explanation does not necessarily suffice to distinguish problem agendas and thus the differences regarding *when* the phenomena 'demand' explanation in the history of biology cannot alone serve as a basis for separating the

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[63] The historical situation in the early 19th century is less clear regarding innovation and novelty than this implies. Comparative morphological investigation prior to 1850 might be interpretable as concerned with the problem agenda of innovation and novelty but there remains a historical discrepancy because the phenomena related to the problem agenda of adaptation were recognized as requiring explanation much earlier in history.

[64] The historiographic issue that the problem agenda may have been captured with different terminology in the past is treated in chapter 4.

problem agenda of adaptation from that of innovation and novelty. The second main reason for distinguishing adaptation from evolutionary innovation and novelty is philosophical, drawn directly from existing resources in biological theory, and constitutes the shared theoretical constraints needed for distinguishing the two problem agendas. Lewontin influentially argued that there were three critical conditions for natural selection to operate in populations of organisms: (i) variation, (ii) this variation makes a differential contribution to fitness, and, (iii) this variation is heritable (Lewontin 1970). This formulation and its possible deficiencies have led to numerous profitable discussions usually considered under the theme of the 'units of selection' debate (Lloyd 1989, 1992; Wimsatt 1980a, 1980b). Zeroing in on these three features we can observe that adaptation takes on the second condition explicitly, because differential fitness effects will be a function of an organism's selective environment (*sensu* Brandon 1990). In contrast, innovation and novelty concerns part of the first condition; i.e., how a particular kind of variation came into being at definitive junctures of time in the phylogeny of species. The existence of the evolutionary innovation or novelty today (e.g. vertebrate jaws) is testimony to the fact that the three conditions were met. But notice that an account of the *origin* of 'new' variation is not required for natural selection to operate (Endler 1986). *That* the three conditions were met does not answer *how* they were met, particularly how the variation that could have had a differential fitness contribution and been heritable originated in a particular population of organisms. Variation is required for evolution to occur, and understanding evolution by natural selection contributes to explanations of adaptation, but no understanding of the origin of new variation is required. It only needs to be *present* as a boundary condition on the operation of natural selection (cf. Sterelny 2000).

Using the tripartite conditions for the operation of natural selection lets us return to Aristotle's strategy for distinguishing scientific problems. Following the example concerning increased Nile river flow at month's end, we can pose an initial problem with respect to some adaptive feature of organisms: 'why did natural selection preserve this particular kind of variation at a particular phylogenetic juncture?' The answer following Lewontin's conditions is 'because this particular kind of variation existed, positively contributed to fitness, and was heritable at the phylogenetic juncture.' Notice now that this answer begets three new problems: (a) why did this particular kind of variation exist at the phylogenetic juncture? (b) why did this kind of variation positively contribute to fitness at the phylogenetic juncture? and, (c) Why was this kind of variation heritable at the phylogenetic juncture? The first of these gets us closer to the problem agenda of innovation and novelty, which is concerned with how particular kinds of variation arose at key phylogenetic junctures. Adaptation concerns how this variation positively contributed to fitness. We can extend this line of reasoning by considering the old debate regarding the relation between microevolution and macroevolution.

Although much ink has been spilt over whether microevolutionary processes can fully account for macroevolutionary phenomena (without the need to invoke species selection explanations), less attention has been paid to how most researchers willingly differentiate between microevolutionary and macroevolutionary phenomena (cf. Jablonski 2000). We can specify these differences in emphasis with the tripartite conditions of natural selection. Microevolutionary phenomena have been approached with questions focusing upon fitness differences and the heritability of variation (mutation), leaving the origin of variation unexplained as long as its presence is reliable. Macroevolutionary phenomena have been tackled through attention to the origin of variation (especially novelties), largely assuming fitness differences and heritability of variation (except for discussions of species selection).

In principle, the emphases could be brought together and certain theoretical strategies are amenable to a merger. For example, dissecting the mapping relations between genotype and phenotype is an attempt to understand how variation at the heritable genetic level (mutation) translates into the origin of variation at phenotypic levels of organization (Fontana and Schuster 1998b; Wagner and Altenberg 1996; cf. Stern 2000). But this kind of study also requires attention to more than mutation because of epigenetic processes that lead to morphological variation. Any conclusions must also be extrapolated to past historical junctures if we are attempting to explain the origin of a particular feature, such as vertebrate jaws. This kind of research is still in its infancy and its absence is conspicuous: "a century and a half after Darwin, we still do not have a comprehensive theory of phenotypic variation" (Hallgrímmson 2003, 375). One feature of interest related to novelties in this regard is how qualitative variation is produced at the phenotypic level, observed in polymorphisms or polyphenisms that are not simply quantitative differences.

Thus far the argument might be construed as transferring an evolutionary problem into the domain of developmental biology. While it is true that the problem agenda of innovation and novelty properly includes how variation originates, which is part of the problem agenda of organismal ontogeny that concerns how both variation and similarity are generated (cf. Wagner and Altenberg 1996), the problem agenda of innovation and novelty demands a component of phylogenetic or evolutionary, rather than merely ontogenetic, time. Consider again the oft-repeated claim that what makes the issue of innovation and novelty distinct is that it concerns qualitative variation: "quantitative change is only part of the story of evolution, for it does not address the question of the origin of discrete (qualitatively different) novelties" (West-Eberhard 2003, 6; cf. Müller 1990; Müller 2002; Müller and Wagner 2003). The origin of qualitatively distinct variation within a generation alone, including the study of phenotypic plasticity, does not alone constitute the problem agenda of innovation and novelty, although it provides materials necessary for tackling it. There is always a geological time slice that contains an ancestral character and derived character that are not related by quantitative variation. "Novelty always represents a qualitative departure *from the ancestral condition*, not merely a quantitative one" (Müller and Wagner 2003, 221, my emphasis). The origin of discrete variation *spatially* concerns the problem agenda of organismal ontogeny whereas the origin of qualitative (discrete) variation *temporally* falls within the problem agenda of innovation and novelty. The difference is critical because the temporal dimension emphasizes what is in need of explanation: at 'unique' temporal moments in the history of life, how did one system of variation exhibited in a lineage generate a new feature that appears to lie outside of the 'normal' range of variation discernable in developing organisms observed today? It highlights discrepancies between states of variation in the past and in the present, making an explanation of the origin of evolutionary novelty require more than developmental biological investigations. We return to the variation origin question drawn out of the tripartite conditions for the operation of natural selection: 'why did this particular kind of variation exist *at the phylogenetic juncture*?'

What does it mean to say that a feature is outside the normal range of variation or that there is a discrepancy between states of variation past and present? It would seem that the simple passage of evolutionary time is enough to make the distance between features of different taxa outside the normal range of variation. Let us return to the qualitative versus quantitative distinction in the work of Ernst Mayr.

> 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" (Mayr 1960, 351).

Mayr held that a commitment to gradualism implied that definitions of novelty would be similar to definitions of species, always subject to the recognition of hazy intermediate cases resisting obvious categorization. This juxtaposition of defining novelties as qualitatively different phenotypes with a strong commitment to gradualism led Mayr to see the major lines of battle between saltational and gradual accounts of the origin of evolutionary novelties, leading him to define the problem as described above.[65]

One way to tease out 'qualitative origin of variation' apart from an *a priori* commitment to gradualism is to explore 'at a phylogenetic juncture' through operational definitions found in phylogenetic systematics. A 'novel' feature of a taxon in comparison with a set of other taxa in a clade is referred to as an 'autapomorphy': "A derived character or character state (*apomorphy*) that is restricted to a single *terminal taxon* in a data set" (Kitching *et al.* 1998, 200). If the character state is 'digit number' and other taxa in the data set have four digits, which represents the ancestral character state, then a single terminal taxon with five digits means that the character state is an autapomorphy. This gives us a more operational meaning for 'qualitative origin of variation at a particular phylogenetic juncture' but it leaves one primary difficulty. If the single terminal taxon had three digits, then the *lack of a digit* would equally be considered an autapomorphy. The absence of an entity would be considered a novelty (Müller and Wagner

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[65] "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, 357).

1991).[66] Thus, the determination of a feature as autapomorphic is a necessary but not sufficient condition for isolating the relevant qualitative variation at a phylogenetic juncture.

We have circuitously returned to the need for a mechanistic explanation of the origin of variation (not its absence) via developmental processes. Autapomorphies are not equivalent to novelties (or innovations) because an explanation of the causal production of relevant variation is ignored in a purely systematics-based approach (revealed in the operational equivalence of the presence and absence of qualitative variation). The demand for a developmental, mechanistic account of variation indicates that the origin of qualitative variation at particular phylogenetic junctures involves the thesis that discrepancies between two observed states of variation are the result of many nontrivial changes or the overcoming of developmental constraints or bias (Arthur 2004a, 2004b; Müller and Wagner 1991; Müller and Wagner 2003; Stadler *et al.* 2001). Although we lack a robust account of how morphological variation originates developmentally (Hallgrímmson 2003) or the nature and role of developmental constraints (Schwenk and Wagner 2003), what counts as 'nontrivial' can be made more rigorous in certain simple cases such as RNA secondary structure (Fontana 2002; Fontana and Schuster 1998a, 1998b; Stadler *et al.* 2001).

The conceptual point concerns what might be termed 'developmental accessibility' (cf. Fontana and Schuster 1998a; Stadler *et al.* 2001). Mayr reduced the problem to one of gradualism versus saltation because he conceptualized the origin of the qualitatively distinct novelty as a transition from one phenotypic state to another (from 'phenotype A' to 'phenotype B'). Understood in this manner, the issue *just is* whether the transformation series between the phenotypic states was continuous or not. But the concern about generating variation through

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[66] This also holds for synapomorphies (shared derived characters), which are often equated with homologies. On this equivalence, the shared derived *absence* of a character counts as a homology (Müller 2003b; Müller and Wagner 1991).

developmental processes means that the origin of a qualitatively distinct novelty actually concerns the transition from one set of mapping relations ('→') between genotype and phenotype to another (from 'genotype A → phenotype A' to 'genotype A' → phenotype B').[67] Even if the transition between the phenotypic states is completely 'gradual', this does not tell us how much change was required in the developmental processes to generate the new phenotypic state. Developmental accessibility is a measure on the difficulty of this change in developmental processes. The inability to produce these kinds of phenotypic changes in laboratory settings is one way of beginning to understand qualitative origin as developmental inaccessibility.

A related factor for tracking developmental inaccessibility is the absence of known transitional forms in the fossil record. There is a triangulation between an ancestral state of variation, a derived state of variation, and the absence of transitional fossil forms that speak to the nature these differences. The connection between the two states of variation is one of qualitative difference that appears to be the result of many different, nontrivial developmental changes (overcoming a developmentally inaccessible outcome). An epistemological gap obtains between these states of variation and the absent fossil forms regarding the developmental transition. Often this triangulation is instantiated in debates about the very nature of the ancestral state of variation at the phylogenetic juncture since it is modeled on contemporary organisms that are highly derived in the absence of fossil forms.

Using our initial description of a problem agenda, we can begin to flesh out the problem agenda of evolutionary innovation and novelty as a distinguishable set of related phenomena (derived, qualitatively new traits) that pose a suite of intertwined research questions (mechanistic origins of variation at particular phylogenetic junctures), which are investigated with the aim of

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[67] Because epigenetic relations can be the mechanism of difference in mapping relations, it is not formally required that there be any alteration from genotype A to genotype A', as I have represented it.

providing a satisfactory theoretical framework (a set of generalized answers or explanatory framework) capable of addressing all of the component phenomena (e.g. neural crest cells, bone, flight, jaws, feathers, endothermy). This provides us with a skeleton for criteria of explanatory adequacy but does not give all of the detail needed. For example, mechanistic explanations of the origins of variation will require a contribution from developmental biology but the nature of that contribution is unclear. In part this is because we need to broach the topic of what is involved in these mechanistic explanations. Highlighting 'phylogenetic juncture' shows that we will need to pay attention to the taxa that we use to evidentially support developmental explanations of variation, especially whether findings from model organisms can be brought to bear on the origin of evolutionary innovations and novelties.

2.3.1.1. Two Caveats on Natural Selection and the Intrinsic/Extrinsic Dichotomy

Although characterizing the problem of innovation and novelty as concerned with the origin of phenotypic variation at particular phylogenetic junctures distinguishes it from the problem of adaptation, it does not thereby denigrate or eliminate the explanatory role of natural selection. This can be seen via Schwenk and Wagner's synoptic discussion of the concept of 'constraint' (Schwenk and Wagner 2003). In order to keep constraint and selection distinct, many have argued that it concerns biases or limitations on the production of phenotypes (Maynard Smith *et al.* 1985). But canalization and viability selection can be sources of this biasing. It therefore seems difficult to effect the conceptual separation. In the case of the origin of variation involved in the production of innovations and novelties the situation is different. The primary concern is the efficacious generation of phenotypic variability; i.e., not the impossible but rather what is possible and was actually produced. Viability selection is ruled out in this regard and canalization becomes another factor that needs to be considered in understanding potential variation outcomes. Natural selection is a necessary *boundary condition* to the origin of variation; it operates ubiquitously but is not explanatorily relevant to understanding the emergence of particular innovations and novelties (cf. Sterelny 2000).

Finally, a brief interlude on the extrinsic/intrinsic dichotomy is required to prevent a misunderstanding. It may sound as if the separation of adaptation from innovation and novelty is achieved by making the former 'extrinsic' (selection) and the latter 'intrinsic' (variation). There are several reasons why this is a problematic construal. As I have argued elsewhere for the concept EVOLVABILITY, the intrinsic/extrinsic dichotomy fits with a traditional metaphysics of intrinsic properties and extrinsic relations but may not capture the nature of the causal bases of organismal dispositions to generate phenotype variability (Love 2003b). This is most salient with respect to phenotypic plasticity, as environmental (extrinsic) contexts can enormously affect the variation produced by a developmental system (Gilbert 2001; Pigliucci 2001b; Sarkar and Fuller 2003; Scheiner 1993; Schlichting and Pigliucci 1998; West-Eberhard 1989, 2003). It is not that extrinsic determinants of phenotypic variation are excluded by taking natural selection as a background condition but rather that they constitute a different relevant environment of the organism. In Brandon's terminology, the *developmental* environment is what is in view, which only composes a portion of the *selective* environment (Brandon 1990, ch. 2). Recognizing the effects of extrinsic factors in the developmental environment of an organism's production of phenotypic variation during ontogeny does not commit one to parsing the precise fitness effects of these variants. It only assumes that these variations occur *in* a selective environment where variations will have selective value due to fitness differences.[68]

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[68] Methods in paleoecology can identify features of selective environments at particular phylogenetic junctures (Jablonski 1993; Jablonski and Bottjer 1990; Jablonski and Bottjer 1991; Jablonski, Lidgard and Taylor 1997).

2.3.2. Characterizing the Problem Agenda

Assuming then that the problem of innovation and novelty is distinct, what are its main components and contours? There are at least three basic dimensions that come into focus: (a) the origin of functions versus forms, (b) the level of biological hierarchy, and, (c) the generality of theoretical and experimental investigations of particular functions and forms at different levels of organization. Each of these is considered below, respectively.

2.3.2.1. Form and Function

The venerable form/function dichotomy is a deeply entrenched tool for conceptualizing organisms in biology. E.S. Russell, one of its most careful students, refers to it in the following manner: "The main battle-ground of these two opposing tendencies is the problem of the relation of function to form. Is function the mechanical result of form, or is form merely the manifestation of function or activity?" (Russell 1982 [1916], ix). Since the *relation* between them lies at the heart of this conceptual tool, it may be more appropriate to see it as an enduring dialectic rather than a dichotomy (Padian 1995).[69] Many discussions make no special distinction in labeling the origin of a particular function an innovation rather than a novelty or *vice versa*, and similarly for the origin of forms. Making a terminological separation is conceptually useful because it highlights methodological asymmetries between explaining the origin of form and the origin of function, as well as revealing a lack of attention to their necessary interconnections. 'Innovation' should be taken to concern the origin of functions and 'novelty' should refer to the

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[69] C.P. Snow's warnings should be heeded: "Attempts to divide anything into two ought to be regarded with much suspicion" (Snow 1998 [1959], 9). Oyama has pointed out a number of ways in which dichotomies can be pernicious in biological research (Oyama 1992). The important difference in the present instance is that the form/function distinction is unified under a more general problem category, *character*, thereby retaining a focus on the important interrelations between them and not artificially segregating them from one another (see below).

origin of forms. By form I mean the material composition and arrangement, shape or appearance of organic materials (Bock and von Wahlert 1965). By function I intend activities at any level of organization performed or displayed by organisms (Dullemeijer 1974, 1981; cf. Gans 1969).[70] This separation opens new conceptual space, as indicated by comparing an extant definition of novelty with a parallel one for innovation.

> A morphological *novelty* is a structure that is neither homologous to any structure in the ancestral species nor homonomous to other structures of the same organism (Müller and Wagner 1991, 243, my emphasis).
>
> An organismal *innovation* is a function that is neither extant in the ancestral species/lineage nor operational elsewhere in the functional context of the same organism.

The second definition complements the first but also raises interesting issues about how to understand notions of 'functional homology' (or better, the homology of functions) (Greene 1994; Lauder 1994). It also is a reminder that if we have provided a solution to how a morphological structure was generated at a particular phylogenetic juncture, we will still need an account of how specific functions were generated at this or other related phylogenetic junctures in order to adequately address the problem agenda of evolutionary novelty *and* innovation.

The separation of innovation (function) and novelty (form) along this axis is not meant to bifurcate the problem. This distinction operates within a common problem, clarifying biological discourse and stressing the fundamental connection between forma and function. It can be gathered under the unwieldy phrase 'the problem of unique apomorphic character origination. "Unique" is intended to capture the qualitative 'newness', relative infrequency, and distinctness of the kinds of events under consideration. "Apomorphic" refers to a derived rather than ancestral feature; the issue is how new structures and functions come into existence in

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[70] In the terminology of the philosophical literature on function, this is not an etiological notion of function but rather one concerned with causal role (Amundson and Lauder 1994).

phylogenetic time. (This formally distinguishes it from the problem agenda of organismal ontogeny.) “Character” is used to join the forms and functions together into complexes that can potentially serve biological roles (*sensu* Bock and von Wahlert 1965). It is not a coincidence that providing an operational definition of characters in biological study is involved.[71]

> How do characters come into existence during the course of evolution? In the context of the evolutionary process, characters are historical individuals, such as species and clades, which have a definite beginning and potentially an end. Since characters are expected to be conservative with respect to certain properties, how did these conservative properties come into existence? This question is called the innovation problem in evolutionary biology… Arguably this is the most challenging and exciting problem in the evolutionary biology of characters (Wagner 2001a, 10).

Characters serve as units of integration for form and function features in the problem agenda of innovation and novelty; that is, characters theoretically unite form and function in the investigation of their origins.[72] “Origination” demarcates the key issue of how new, shared derived features arise from how they are stabilized, maintained, or further modified. It comprises a subset of the problem of the origin of variation and thus natural selection is assumed to be present but not explanatorily utilized. The problem agenda of evolutionary innovation and novelty takes natural selection as a boundary condition, *just as* the problem agenda of adaptation takes the origin of new variation as a boundary condition (Sterelny 2000).

One consequence of the terminological distinction between innovation (function) and novelty (form) when juxtaposed with the distinctness of the problem agenda of adaptation is that the important idea of a *key innovation*, referring to the capacity of a morphological change to elicit a significant adaptive radiation (Galis 2001; Galis and Drucker 1996; Hunter 1998; Hunter

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[71] “[A] biological character can be thought of as a part of an organism that exhibits causal coherence to have a well-defined identity and that plays a (causal) role in some biological processes” (Wagner 2001a, 3; cf. Fristrup 1992; McShea 2000, 2001; McShea and Venit 2001; Wagner and Laubichler 2001).

[72] The significance of this integrative role will be highlighted in Chapter 6 (cf. Kauffman 1970; Wagner and Laubichler 2001; Weibel 2000; Wimsatt 1976).

and Jernvall 1995; Liem 1973, 1980, 1990), is not formally part of the problem agenda of innovation and novelty. The adjective ‘key’ foregrounds natural selection and explicitly broaches issues within the domain of the problem agenda of adaptation. What is in view with key innovations is not how an innovation originated but what happened after it did, namely through its differential effects on fitness and evolvability.

Bracketing key innovations is incongruent with other arguments for the distinctness of a problem agenda of innovation and novelty.

> Arguments in favor of the distinctness of innovations from other forms of phenotypic evolution have been made on two grounds: (1) the origin of novelty may include different mechanisms than the mutations underlying variation and adaptation, and (2) certain phenotypic changes may have more important and long lasting consequences for the dynamics of evolution (Müller and Wagner 2003, 219; cf. Müller 2002).

On the view presented here, the consequences on subsequent evolution (item 2) are *not* formally part of the problem agenda of innovation and novelty. Attending to these consequences draws our attention away from origination to diversification, maintenance, and proliferation (a different problem agenda). Therefore key innovations, as such, do not afford a reason to keep adaptation concerns separate from those in the domain of the problem of innovation and novelty.[73] The claim that the origination of innovations and novelties may involve different mechanisms also does not mesh with the account proposed here. Since my analysis focuses on the questions being asked, it does not require in advance the operation of different mechanisms, which are formally ‘answers’ to the questions being posed. My definition of the problem agenda of innovation and novelty as comprising a subset of the problem of the origin of variation with a temporal

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[73] The issue of ‘exaptation’ is purposely ignored here (Gould and Vrba 1982). The concept of EXAPTATION foregrounds the explanatory role (or lack thereof) of natural selection in order to distinguish historical emergence from current utility. I am not concerned with spandrels and non-adaptation (Chipman 2001; Gould and Lewontin 1978). Judgments about the nature of an ‘exaptive pool’ (inherent potentials vs. available things) (Gould 2002, ch. 11) concerns what is selectively accessible, i.e. it focuses on what variation is present. It does not address the mechanistic basis of *how* the variation arose, though it makes more explicit the need to attend to the question.

dimension focusing on discrepancies in states of variation past and present demands an inquiry into the possibility of different mechanisms generating new forms and functions in the history of life. The *actual* explanatory relevance of different mechanisms is decided empirically.

2.3.2.2. Level of Biological Hierarchy or Organization

Explaining evolutionary innovations and novelties requires attention to where they reside in the hierarchical organization of organisms and populations: "The origin of evolutionary novelty involves changes across the biological hierarchy: from genes to cells to whole organisms and ecosystems" (Shubin and Marshall 2000, 324). Although a number of natural 'levels' are frequently utilized (e.g., gene, cell, tissue, organ, organism, species), there is no *a priori* commitment to primary or natural levels (cf. Korn 1999, 2002; Salthe 1985, ch. 6). For our purposes, there are two kinds of relevant hierarchies, extracted and combined from a number of authors who have discussed the nature of biological hierarchies and their evolution (Ahl and Allen 1996; Craver 2001; Grene 1987; Korn 1999, 2002, 2004; McShea 1996, 2000, 2001; Pattee 1973; Salthe 1985, 1993; Simon 1977 [1973]-a; Valentine and May 1996; Whyte, Wilson and Wilson 1969; Wimsatt 1976a, 1976b, 1986, 1997). Each of these can be described either in terms of developmental time within a single generation or evolutionary time across generations (cf. Newman 2003). The first kind is compositional (or scalar) hierarchies understood as part-whole relationships. The second is procedural (control or organizational) hierarchies, which call attention to process dependence. If we map these onto the form-function distinction from the previous section, and consider them occurring in developmental space versus evolutionary time, eight distinct possibilities emerge:

1. Compositional form hierarchy in developmental space: specific form features are nested within ('subparts of') the morphological novelty during ontogeny within a single generation (e.g. cells aggregate into tissues; tissues aggregate into organs).
2. Compositional form hierarchy in evolutionary time: specific form features are nested within ('subparts of') the morphological novelty during the evolutionary process across generations (e.g. existence of cells was required before aggregations of cell types or tissues could be formed).
3. Compositional function hierarchy in developmental space: specific function features are nested within (subparts) of the organismal innovation during ontogeny within a single generation (e.g. individual muscles cells must be able to contract prior to an entire muscle contracting).
4. Compositional function hierarchy in evolutionary time: specific function features are nested within (subparts) of the organismal innovation during ontogeny within a single generation (e.g. existence of muscle cell function precedes origin of muscle function).
5. Procedural function hierarchy in developmental space: specific function features must activate serially or jointly prior to the operation of the organismal innovation during ontogeny within a single generation (e.g. folding of the neural tube in vertebrates precedes the detachment and migration of neural crest cells).
6. Procedural function hierarchy in evolutionary time: specific function features must activate serially or jointly prior to the operation of the organismal innovation during the evolutionary process across generations (e.g. gene expression involved in the folding of the neural tube must originate prior to gene expression involved in the detachment or migration of neural crest cells).
7. Procedural form hierarchy in developmental space: specific form features must occur serially or jointly prior to the generation of the morphological novelty during ontogeny within a single generation (e.g. a tubular structure must exist in the embryo before it can differentiate into a multi-part gut).
8. Procedural form hierarchy in evolutionary time: specific form features must occur serially or jointly prior to the generation of the morphological novelty during the evolutionary process across generations (e.g. a relatively undifferentiated through-gut must have originated prior to a more morphologically differentiated digestive tract).

Delineating these logical possibilities forces attention to the different ways that variation relevant to the origin of innovations and novelties can appear at particular phylogenetic junctures, which become more complex to disentangle at higher levels of organization, whether compositional or procedural. Form features not strictly subject to a superordinate relation of compositional nesting but resulting from epigenetic dynamics such as self-organization phenomena (‘attractors’), can be understood as resulting from a procedural hierarchy rather than (as is typical), a compositional one (cf. Bar-Yam 1997; Kauffman 1993; Salthe 1993, ch. 4).

The explanatory demand invoked here is an old one.[74] The citation of a mutation causing particular phenotypic effects will not in itself be an adequate explanation until the developmental processes by which the genetic change initiates a cascade of causal differences that eventuate in phenotypic differences are elucidated (cf. Stern 2000). Similarly, a full account of the developmental processes generating particular forms is inadequate if there is no account of how the phenotype is integrated to perform organismal functions. This is not about reductionism; the exclusion of the developmental mapping for the origin of variation leaves out the ‘middle’ causal processes or mechanisms (Brandon 1996). Consequently, there is no need to engage debates about whether there are emergent properties in these hierarchies, because if the explanatory task is executed, then attention will have been paid to appropriate materials for making this assessment, depending on one’s account of emergence (Bunge 2003; Kline 1995; Korn 1999,

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[74] “The task of science is not complete until it has followed phenomena through all levels of hierarchy, up and down as far as possible, and … tied them all together …working down from … the level of the individual to those of chromosomes and genes and to the chemistry of these, and up again into the physiology of gene action at the levels of cell, tissue, organ, and individual and finally to the properties of populations” (Wright 1964, 288).

2002, 2004; McShea 2001; McShea and Venit 2001; Newman 2003; Salthe 1985; Wimsatt 1976a, 1986, 1997).[75]

2.3.2.3. Degree of Generality

The final dimension characterizing the problem agenda of innovation and novelty is the degree of generality. For a form (*x*), function (*y*), or character (*xy)* at a specified ('focal') level of the biological hierarchy, to what degree can the explanatory principles invoked be generalized to other cases of innovation and novelty? By generalization I mean any description or explanation that is applicable across multiple domains in the sense of capturing repeatable natural patterns in an economical epistemic format (cf. Darden 1996). Generalizations can be assessed along at least three dimensions: abstraction (how much a generalization is able to ignore particular details or variation), stability (how resilient the generalization is to changes in causal structures and relations), and strength (how frequently the generalization holds, deterministically or probabilistically, from high to low) (Mitchell 2000).[76] From our analysis thus far of the problem agenda of innovation and novelty, generalizations will need to be concerned with the *transferability* of form explanations to function (and *vice versa*), explanations at one level of a hierarchy to another, as well as explanations derived from one species of organism to another. In the latter case, we join the issue of model organism use in contemporary biology (Bolker 1995; Hanken 1993; Schaffner 1998a, 1998b).

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[75] The recognition that what we mean by hierarchies is broader than part-whole relations avoids the concern that levels talk is somehow fundamentally confused (Wilson 2003). The problem is assuming that mereology is the primary concern when thinking about hierarchical structures in biological entities rather than the myriad of logical possibilities detailed above. Additionally, attention to the construction of hierarchies during ontogeny removes the seemingly puzzling feature of 'entwinement' between levels because attention is being paid to the construction of part-whole hierarchies (Wilson 2003), revealing how exactly they are related, something not captured by a static evaluation of relationships between levels.

[76] Laws can be considered limiting cases, where the generalizations are universally applicable because they are highly abstract, stable, and strong.

Although model systems are necessary for laboratory experimentation, whether causal generalizations about developmental processes that produce variation have broad scope must be evaluated, since we eventually want to make analogical inferences to other organismal systems or generalize the results (Burian 1993a). But in the present case the issue is not broad scope but *relevant* scope; i.e., we want to know if the study of the origin of variation in model systems is relevantly applicable to the particular phylogenetic junctures under scrutiny. Because of this, we might begin with an *a priori* expectation that generalizations derived in explaining particular innovations and novelties will not have broad scope (either due to instability or lack of strength) because of the 'uniqueness' aspect in the problem agenda. This expectation is partly correct but the complex reasons why need to be detailed.

With the prevalence of molecularization in recent life science research (cf. Fraser and Harland 2000; Morange 1998), there has also been a trend toward explanations that invoke entities and activities at lower levels of biological hierarchies in part because of the ease with which they are experimentally manipulated and their apparent generality. Generalizations about the behavior of molecular biological entities are highly stable across different species of organisms and are instantiated probabilistically with a high frequency. Thus, for forms, functions, and characters at 'low' levels of compositional and procedural hierarchies, such as gene expression or protein complexes, the generality can be quite high. This implies that explanations of the origin of evolutionary innovations and novelties at these levels can be generalized. For example, understanding the origin of a particular gene (structure – form) by duplication is applicable to a whole host of other gene origin events. Similarly, the origin of a particular function, such as DNA binding in a transcription factor protein, will be widely applicable because of the universality of DNA among organisms.

But, paradoxically, for forms, functions, and characters at 'high' levels of compositional and procedural hierarchies (e.g. jaws or the tetrapod limb) generality is lower. In part this is because these entities exist at the end of complex combinations of compositional and procedural hierarchies that occur in development and are often not widely instantiated in other species. This leads us to the observation that the molecular level generality is *non-transitive* (cf. McShea 2001; Salthe 1985). If you understand something about the production of variation at a molecular level, this does not automatically translate into an understanding of variation origin at higher levels of organization. The empirical evidence for this non-transitivity has been growing and includes the dissociation of homologous gene expression from homologous structures (True and Haag 2001; Weiss and Fullerton 2000; Wray 1999a), co-option and convergence of gene expression (Raff 1996; True and Carroll 2002), and the details of epigenetic interactions occurring during ontogeny (Müller 2003a; Oster *et al.* 1988; cf. De Visser *et al.* 2003; Kitano 2004; Stadler *et al.* 2001).[77] I term the non-transitivity of molecular level generality the 'molecular paradox' because it highlights how the amazing generality of molecular level processes pertinent to understanding the origin of innovations and novelties across various taxa does not translate into an understanding of higher level processes within and across taxa.

Recognizing the molecular paradox recovers why biologists might argue for the possibility of different mechanisms for the origin of variation (other than mutation) as a rationale for keeping innovation and novelty distinct. Arguing for their distinctness on this basis is motivated by the very real empirical concerns that generate the molecular paradox. But my analysis does not require the existence of the molecular paradox in order to keep the problem agenda of evolutionary innovation and novelty distinct. Even if there were no other mechanisms

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[77] Some of the empirical evidence has been available for a long time, such as in Spemann's 1915 discussion of amphibian lens regeneration and homology (cf. Laubichler 2000). It was also included in one of the most widely cited discussions of homology prior to the emergence of Evo-devo (de Beer 1971).

than genetic mutations underlying phenotypic variation, it would still be necessary to demonstrate this by detailing mechanistic connections during ontogeny. Thus, if the assumption made by proponents of the Modern Synthesis about the straightforward nature of the mapping relations between genotype and phenotype had turned out to be correct, there would still have been an explanatory demand to articulate the mechanistic origins of phenotypic variation that derived from underlying mutations (Stern 2000).

Paying attention to these differences in generality across levels is also important because many of the causal generalizations in biological science are characteristically inter-level (Craver 2001; Hartwell *et al.* 1999; Oltvai and Barabåsi 2002; Schaffner 1993a; Schaffner 1993; Wimsatt 1976b). The generalizations being sought for evolutionary innovations and novelties will likely be "a complex web of inter-level causal generalizations of varying scope" (Schaffner 1993b, 333; cf. Schaffner 1993a, ch. 6, 9) and thus the degree of generality is intimately connected with the features of the levels that enter into these 'inter-level' generalizations.[78]

Generality can be purchased by other means than molecular level mechanisms. With respect to the origin of function, biomechanical or physiological principles derived from physical equations of Newtonian bodies can be utilized. With respect to form, physical principles of 'excitable soft matter', such as cohesivity, viscosity, elasticity (Newman 1994; Newman and Müller 2000), morphogenetic processes, such as fluid forces in organogenesis (Hove *et al.* 2003) or 'construction rules' (Oster *et al.* 1988), and the dynamics of complex systems (Bar-Yam 1997; Kauffman 1993) offer explanatory principles with broad scope. Also, any generalizations must take into account temporal and spatial *variation* in the origin of innovations and novelties, such

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[78] I am not committed (*pace* Schaffner) to the ultimate unilevel reduction of these inter-level explanations. Inter-level causal generalizations are not proxies, ultimately to be replaced by completed, lower level causal generalizations. The molecular paradox actually militates against this.

as the large amount of morphological novelty during the Cambrian radiation or in tropical biogeographic regions (cf. Jablonski 1993, 2000).

2.3.2.4. Analytical Results

We can now return to our analogical probing of van Fraassen's theory of explanation to explicate the problem agenda. First, we have a set of *explanandum* phenomena: neural crest cells, bone, flight, jaws, feathers, and endothermy. These encompass form, function, and character domains and exist at different levels of biological organization. Second, there is a primary presupposition to the problem agenda: these phenomena are not artifacts and distinctly different from 'microevolutionary' phenomena. This reality was underwritten by drawing attention to the discrepancy between states of variation past and present while simultaneously recognizing that this does not imply saltation as the actual mechanism of origination. Third, there is a set of interrelated questions. Some of these include:

- How do new tissue types arise mechanically during development in phylogenetically appropriate organisms?

- Does the origin of functional variation proceed by different principles than the origin of structural variation?

- Is the prerequisite variation in phenotypes initially dependent on genetic mutation, epigenetic dynamics, or both?

Although there is not anything approaching a complete solution on offer, partial solutions have been proposed. For example, Newman and Müller answer the last question in favor of epigenetics: prerequisite variation in phenotypes is initially dependent on epigenetic dynamics, especially during early periods of organismal evolution. Genetic mutation is a source for the secondary hardwiring of these novel phenotypes (Newman and Müller 2000). At the same time we can also observe the presence of a corrective solution put forward by some neo-Darwinian biologists to the effect that innovations and novelties are not distinct from other 'variation' phenomena because they are typological constructs, i.e. artifacts (Cracraft 1990).

The relevance relation was purchased with theoretical constraints found within evolutionary theory (the tripartite conditions for the operation of natural selection), which provide the context for the individuation of the problem agenda of innovation and novelty as concerning the origin of variation at particular phylogenetic junctures. This individuation also indicates that natural selection is *not* in the contrast class of possible answers. Once individuated, the problem agenda required further detailed characterization in order to provide criteria for assessing solutions. The three dimensions characterized composed a basic set of criteria for explanatory adequacy for integrated explanations of evolutionary innovations and novelties. Our individuation of the problem agenda as the origin of qualitative variation at particular phylogenetic junctures informed us that developmental biology is necessary to explain evolutionary innovations and novelties since the problem agenda concerns the mechanistic generation of variation. We also made a terminological distinction between innovation (function) and novelty (form), which in part helped clarify that 'key innovations' are not properly part of the problem agenda since they foreground the operation of natural selection in terms of subsequent consequences of innovation and novelty (e.g. adaptive radiation). Our characterization of the problem agenda forces us to attend to both form and function through integrative character 'units', at all appropriate levels of biological organization, and with an eye to the degree of generality of principles invoked for form or function, at particular hierarchical levels, in different model systems being studied.

It is now more perspicacious why explanations of evolutionary innovations and novelties require multidisciplinarity. In order to have conceptual resources for form, function, and characters, at all levels of the biological hierarchy with sufficient generality, a number of disciplines need to be synthesized in order to produce integrated explanations. The molecular paradox highlights that strong generality across taxa for the molecular level does not translate into generality across taxa, across hierarchical levels. The component of phylogenetic juncture specifically highlights the need for contributions from systematics and paleontology. Recognizing the distinctness of the origin of organismal innovations requires more attention to the ontogeny of function in addition to form. A full detailing of these various consequences and others, as well as more specific recommendations derived from this analysis of the problem agenda of innovation and novelty, will be canvassed in Chapter 6.

One can view the accomplishment of this chapter on analogy with Simon's discussion of problem structure: "much problem solving effort is directed at structuring problems, and only a fraction of it at solving problems once they are structured" (Simon 1977 [1973]-b, 310). Whether the solving fraction is small is another matter but the existence of a structured problem with transparent criteria of explanatory adequacy is a clear philosophical achievement relevant to ongoing research in Evo-devo on evolutionary innovations and novelties. Another way to phrase this achievement is that the interdisciplinary task has been made 'conceptually transparent' (Broido 1979); i.e., we have characterized what it is that needs to be explained.

Possessing an account of problem agendas and having individuated and characterized the problem agenda of innovation and novelty, it is useful to briefly sketch its role in identifying conceptual clusters. (The reconstruction of conceptual clusters will be undertaken in Chapter 6.) First, our explanatory target concepts are EVOLUTIONARY INNOVATION or NOVELTY, which can be considered entities (form – novelty), activities (function – innovation), or entity/activity combinations (characters – form/function complexes). Thus, the conceptual clusters isolated will be those concepts jointly deployed in the explanation of these features. Since we are assuming explanations are causal, we will observe explanations that attribute the origin of these features to particular entities, processes, or their properties, in particular spatiotemporal and causal relations to one another. Our analysis in this chapter draws attention to whether forms (entities) or functions (activities) are in view, what level of biological organization the innovations or novelties occur at, as well as the level of the evidential and causal concepts, and the ability to generalize data culled from one species to appropriate phylogenetic junctures.

2.4. Problem Agendas and Problems as Units in Philosophy of Science

The focus of this chapter thus far has been on the idea of a problem agenda and demonstrating its utility through application to the issue of articulating criteria of adequacy for explaining the origin of evolutionary innovations and novelties. We began the chapter with a brief set of arguments for why problems are favorable units of analysis but did not address earlier attempts at using problem-related units in philosophy of science. The subsequent sections treat three related topics: the relationship between problem agendas and other problem-related units offered by philosophers of science such as Popper and Laudan; the similarities and differences between Shapere's notion of 'domain', Darden and Maull's 'fields', and problem agendas; and, the differences between discussions of 'scientific values' in philosophy of science and my focus on problem agenda characterization as making criteria of explanatory adequacy explicit.

2.4.1. Prior Accounts of Problems in Philosophy of Science

Over the past forty years, a number of different units of investigation have been postulated for understanding the nature of scientific knowledge and its changes through time (McGuire 1992). Famous examples include Kuhnian paradigms (Kuhn 1996 [1962/1970]) and Lakatosian research programmes (Lakatos 1970), which emphasize some form of shared epistemic framework among a delineated community of scientists, as well as various interpretations of explanations, hypotheses, models, and theories (see, e.g., Salmon 1989; Suppe 1977, 2000). Others have offered 'styles' of thinking or reasoning (Crombie 1994; Davidson, A. I. 2001, ch. 5; Fleck 1979 [1935]; Hacking 2002b; Harwood 1993) #5594], or 'ways of knowing' (Pickstone 2001) for analyzing methods used in science to obtain knowledge or understanding.[79] A basic feature of these studies (in both history and philosophy of science) is that the investigative units are in terms of resources (methodological or substantive) used to explain or the outcome (product) of successful explanations (e.g. theories). Less attention has been paid to units of investigation highlighting what is in need of explanation or scientific *problems*.[80]

As noted in the introduction, there are many reasons to favor analyses in terms of problem units. I am by no means the first to be concerned with problems as units of analysis in philosophy of science. Problems were explicitly discussed in several key texts in philosophy of science during the 1970s.[81] Attention to the questions driving scientific practice rather than the knowledge structures used to provide answers is discernable in Kuhn's underdeveloped notion of

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[79] This description is illustrative, not exhaustive. Sociologists of science have sought investigative units using social, cultural, and political demarcations (McGuire 1992; Pickering 1992).

[80] "Problems, their structures, relations, and varieties, have received negligible attention in comparison with the enormous effort devoted to the analysis of theories" (Nickles 1978, 134). Units of analysis in terms of how or what is known can be complementary to units of analysis in terms of scientific problems. For example, one could comprehend research programs in terms of their problem solving ability (Frankel 1980; Laudan 1977).

[81] They also received treatment in older literature (Polanyi 1957; Smith, 1945; Somerville 1935).

‘problem fields’ (Kuhn 1996 [1962/1970]), from which some of the concern about non-semantic incommensurability originally arose. Toulmin took genealogies of problems as the core notion in understanding the development of scientific knowledge (Toulmin 1972).

> The source of scientific problems lies, therefore, in a delicate historical relationship between the attitudes of professional scientists and the world of Nature which they study. Problems arise (I say) where our ideas about the world are at variance either with Nature, or with one another: i.e., where our current ideas fall short, in some remediable respects, of our intellectual ideals. … Scientific Problems = Explanatory Ideals – Current Capacities (Toulmin 1972, 151-2).

Toulmin’s equation makes the connection between how (‘explanatory ideals’) or what (‘current capacities’) is known and the unknown (‘scientific problems’) explicit. Scientific problems arise *because of* a gap between current theoretical resources and the natural phenomena to be explained. ‘Conceptual problems’ (distinguished from empirical issues and from formal, mathematical, and semantic problems) are placed into five groups (Toulmin 1972, 177-180):

i. certain phenomena which a natural science can reasonably be expected to explain, yet for which no available procedure yet provides a successful treatment
ii. some phenomena which can be accounted for up to a point using current explanatory procedures, but for which scientists would welcome more complete or more precise explanations
iii. problems arise when we consider the mutual relevance of coexisting concepts within a single branch of science
iv. some problems concern the mutual relevance of concepts from different branches of science
v. problems arise out of conflicts between concepts and procedures current within the special sciences and ideas and attitudes current among people at large

Toulmin’s discussion touches on concerns raised earlier about the nature of problems requiring attention to existing theoretical resources. He also recognizes the importance of focusing on problems themselves as units to track scientific knowledge changes because it brings the differences in theoretical resources between branches of science into relief.

Although Popper discussed scientific problems throughout his career, the account from later publications is discussed here (Popper 1972, esp. ch. 4; cf. Popper 1999a, 1999b). Popper's basic unit is a "problem situation", which is then further decomposed into a "problem", a "framework", and a "theoretical background" (Popper 1972, 164ff). Problems themselves are often simple but their nesting in a theoretical background and existing methodological resources (framework) makes the problem situation very conceptually complex. The relation between problems and solutions is understood as logical and therefore (for Popper) objective (Popper 1972, 156-165). These features exist in Popper's 'Third world'[82] and fit into his method of conjectures and refutations, whereby a problem is addressed with a tentative theory, which is severely tested ('error elimination') and then begets a new problem (Popper 1972, 164). Because of the nature of the problem situation, Popper holds that "most new problems arise out of the criticism of theories: they are internal to theory …the problems are themselves products of theories, and of the difficulties that critical discussion uncovers in theories" (Popper 1999b, 14).

Laudan has also recognized the paucity of studies about problems: "The literature of the methodology of science offers us neither a taxonomy of the types of scientific problems, nor any acceptable method of grading their relative importance" (Laudan 1977, 13). To begin remedying this situation he focuses on a distinction between empirical problems and conceptual problems, where the former refers to "anything about the natural world which strikes us as odd, or otherwise in need of explanation …substantive questions about the objects which constitute the domain of any given science" (15), whose criteria of explanatory adequacy involves the object in the domain under scrutiny (Laudan 1977, ch. 1). Conceptual problems consist of difficulties that arise within particular theories either due to *internal* inconsistencies or opacity of foundational

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[82] 'First world' = 'world of physical events'; "Second world" = 'world of mental events'; "Third world" = 'world of products of the human mind', such as scientific theories.

concepts or *external* conflicts with the conceptual components of other theories (Laudan 1977, ch. 2). Problems always arise within a context of inquiry and thus are partly defined by that theoretical context, even when empirical. Empirical problems can be subdivided into solved, unsolved, and anomalous problems referring, respectively, to whether a theory has adequately addressed a problem or not, and if the latter case holds, whether a rival theory has addressed it.

Following on the heels of these other discussants, Hattiangadi and Koertge have dwelt on the significance of problems as analytical units. Koertge begins with the divergent viewpoints on questions offered by Dewey and Popper, assessing to what degree questions have a subjective versus objective basis.[83] In order to better understand how problems are chosen or deemed significant to pursue, she offers descriptions of problem importance in terms of their impact of on our knowledge (K-importance) and impact on our ability to act (A-value), as well as those pursued for pleasure (pure puzzles; P-value). These problems can be rated in terms of how likely they are to be solved given current methodological resources (S-scale). In contrast to Popper, she acknowledges three main types of problems: those arising from inconsistencies, those arising from incompleteness (both deductive and explanatory), and those arising from systematic flaws. Using the S-scale and K-, A-, and P-valuations, Koertge formulates many different 'rules' about how problems behave in scientific inquiry with respect to importance and solvability.

Hattiangadi launches primarily from Popper, construing problems as logical inconsistencies rather than questions, with the primary aim of understanding what underwrites a choice of particular problems for scientific investigation (Hattiangadi 1978). These inconsistencies are "intellectual" rather than "practical", arising in the context of disciplinary research where one or more existing theories is under construction in order to predict or account

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[83] The work of Koertge reviewed here is currently unpublished but available in manuscript form from her website: http://www.indiana.edu/~koertge/research.html. The manuscript titles discussed here are "Popper and Dewey on Problems" and "The Importance of Scientific Problems".

for certain natural phenomena. His aim is to set forth criteria for deciding between competing theories that recognize the existence of a shared problem but have potentially diverging explanatory desiderata for removing the logical inconsistency (Hattiangadi 1978, 358-361). Hattiangadi thinks it crucial to capture the historical nature of these logical inconsistencies in theoretical research (Hattiangadi 1979). Abandoning Popper's distinction between problems and problem situations, he distinguishes "ordinary" problems from "deep" problems, where the former are unit-structures easily resolved to maintain theoretical economy and the latter are structured by links to historical debates. Different intellectual traditions attempt to pose problems to other competing traditions or solve problems within their own ("discriminatory" problems) and if problems come to be shared between competing intellectual traditions they are said to be "common" (Hattiangadi 1979). Hattiangadi's theory contains many subtleties ignored here and is subject to several criticisms, both in terms of its internal consistency as well as his restriction of problems to logical inconsistencies (Giunti 1988).

Nickles has offered another sophisticated account of problems (Nickles 1978, 1980, 1981), which was originally motivated by a recognition that the reduction of one problem to another problem is an important phenomena in the history of science that is left unanalyzed by accounts of theory reduction (Nickles 1976). For Nickles, "a problem consists of *all* the conditions or *constraints* on the solution plus the demand that the solution (an object satisfying the constraints) be found" (Nickles 1981, 109). Among the constraints he has in mind are logical and semantic constraints (consistency and clarity), general and specific methodological constraints (e.g. simplicity), and reductive constraints such as reducing a problem to a more tractable form (Nickles 1978). He provides a thorough list of conditions on any account of problems, including eleven logical and conceptual requirements, twelve forms of evidence that problems have conceptual depth, and ten forms of evidence that conceptual constraints belong to the problem itself (Nickles 1980, 1981). One conceptual requirement is particularly relevant to the disciplinary syntheses under consideration here: “Two scientists can have the same problem without knowing the same things about it and can approach the problem from different directions, even from different fields” (Nickles 1981, 86). Arguably the most radical move in Nickles’ argument for his ‘constraint-inclusion’ model of problems is that desiderata on a problem solution derived from theories are part of the definition of a problem (“problems are anchored in the theoretical background which is constitutive of them”) and thus problems change frequently and dramatically in the history of science (Nickles 1978, 1980, 1981).

More recently, several authors have fixed on questions as units of analysis in history and philosophy of science. Allchin takes Kuhn’s notion of problem fields and explicates it in terms of defining particular investigative communities (Allchin 1990). Jardine works through the issue of the reality of questions asked in scientific endeavors past and present both at the ‘local’ and ‘global’ level, attempting “a radical shift of concern from the answers and doctrines that have been propounded by the sciences to the questions and problems that they have posed” (Jardine 1991, 2). Using natural history as an exemplar, Jardine argues that the local scenes of inquiry, the communities *where* the questioning occurs, dramatically affect the kinds of questions posed and ignored by researchers. The reality of these questions is dependent on whether there are ‘communal dispositions’ that admit the existence of evidence bearing on those questions. Rheinberger’s discussion of ‘epistemic objects’, which exhibit a dynamic character of productive elusiveness in concrete experimental contexts of laboratory research, is another approach in this vein (Rheinberger 1997).

Each of these authors makes a valuable contribution, and there are others that I have not even touched upon (e.g. Simon 1977 [1972]). Some focus on features not of immediate interest here. Allchin emphasizes how shared problems might define a community, whereas I am interested in accounting for how *different* communities can reconcile epistemological differences when interacting over a common problem. Jardine stresses the locale of inquiry, whereas I am offering an abstract characterization of these problems *apart* from their multiple scenes of inquiry that might produce shared criteria of explanatory adequacy (but see Jardine 1991, ch. 9). Rheinberger concerns himself with the instability of targets of explanation in experimental contexts, whereas my targets of explanation are highly stable rather than dynamically changing.

Among the other discussions from philosophers of science concerned with problems, there are key differences with my account of problem agendas. Almost all of the authors conceive of problems as having unit-structure, highlighted in Toulmin's equation and Laudan's desire to offer a calculi of scientific progress in terms of solved, unsolved, and anomalous problems. Problem agendas do not have this unit-structure and are composed of a variety of questions that are not necessarily essential to the nature of the problem agenda itself. That problem agendas usually are composed of sets of problems navigates two main dilemmas in these accounts of problems. First, no commitment needs to be made to the primacy or relative importance of one 'kind' of problem, as different kinds of problems can be present in a single problem agenda. Since different types of problems compose problem agendas, there is no need to argue that scientific problems are all of a particular sort. Also, the relative importance or solvability of a problem agenda does not turn on the type of problem. This is especially important given the claims that empirical problems such as the demand to explain natural phenomena are less interesting due to a lack of conceptual depth (cf. Laudan 1977; Nickles

1978). Problem agendas have conceptual depth by virtue of encompassing problems of many different types that are coordinated by the presupposition that certain natural phenomena are in need of explanation. Second, problem agendas can be stable because the addition or removal of particular problems or alterations in theoretical frameworks does not routinely call into question the fundamental commitment to explain the natural phenomena. Problem agendas do not exhibit abrupt change as some accounts of problems demand (cf. Nickles 1981, 95ff).

Many of the authors are concerned to explain the growth of scientific knowledge whereas problem agendas are meant to capture enduring phenomena that demand an explanation across theoretical frameworks (successful or not). Problem agendas emphasize criteria of explanatory adequacy explicit in order for different investigative communities to tackle the questions within it. Laudan's main purpose is to analyze research traditions in terms of their problem solving ability (turning unsolved and anomalous problems into solved ones) to get a measure of scientific progress or rationality (cf. Simon, 1977 [1972]). This commitment is widespread in the discussions of problems reviewed here; they aim to elucidate scientific theory-choice in terms of general rational methodological procedures (cf. Giunti 1988; Shapere 1984a). My focus on criteria of explanatory adequacy requires more attention to the specific content of the problem agenda rather than its form. It is a satisficing strategy rather than a generalization strategy (Section 1.3) in that the goal is not to generate general methodological prescriptions for theory choice but to offer concrete criteria applicable to the problem agenda under consideration for ongoing research in particular scientific disciplines.

Other differences emerge from particular pair-wise contrasts. Besides Nickles, very few of the authors are concerned with distinguishing one problem from another. And my discussion of problem agenda individuation differs from that offered by Nickles, despite my appropriation of his constraint terminology. Nickles holds that constraints ‘characterize’ or ‘describe’ the criteria of explanatory adequacy (Nickles 1981, 109),[84] whereas theoretical constraints were used here to individuate the problem agenda, leaving its characterization (and therefore its criteria of explanatory adequacy) as a secondary component of the analysis.[85] Instead of ‘different constraints, different problems’ (Nickles 1981, 111), my account of presuppositions and theoretical constraints allows for the same constraints to beget distinct problems and recognizes the rejection of an explanatory burden (presupposition) within shared theoretical constraints.

2.4.2. Domains and Fields: Units and Relations in Philosophy of Science

In addition to discussions of problems in philosophy of science, two other units of analysis offered by philosophers of science have relevant similarity to the idea of a problem agenda. These are Shapere’s ‘domains’ (Shapere 1977) and Darden and Maull’s ‘fields’ (Darden and Maull 1977). Consideration of these other units also directs us to remark on the relations claimed for these units in scientific knowledge structures.

Shapere’s idea of a ‘domain’ is offered as an alternative way of understanding the nature of theories in scientific endeavors. “If we examine some relatively sophisticated area of science at a particular stage of its development, we find that a certain body of information is, at that stage, taken to be an object for investigation” (Shapere 1977, 518). Domains are characterized as cohesive units in terms of four basic components: (1) the association is based on some relationship between the items; (2) there is something problematic about the body so related; (3) that problem is an important one; and, (4) science is “ready” to deal with the problem. On this

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[84] “The set of constraints thereby determines the admissible solutions to the problem” (Nickles 1981, 113).

[85] Koertge argues that the conflation of constraints and desiderata is a serious flaw in Nickles’ account. In the language used to develop problem agendas, Nickles collapses the distinction between presuppositions and theoretical constraints. He originally kept constraints and desiderata separate (Nickles 1978).

conception the problematic nature of the domain arises from the jointly considered items understood as related. One feature that is germane to the account of problem agendas is that 'readiness' is achieved in part through precision with respect to the statement of the problem or, in my terminology, an articulation of the criteria of explanatory adequacy. Problems can formally arise with respect to the domain itself, a need for a unified explanation or theory of items in the domain, or inadequacies with respect to a theory offered for the items in the domain. With respect to the middle category, he articulates two types of theories that can be offered as explanations of domain items: compositional and evolutionary (Shapere 1977, 533-534). Compositional theories are developed for periodically ordered domains (e.g. periodic table of elements) and evolutionary theories are developed for sequentially ordered domains (e.g. origin of elements in stellar evolution).

Domains differ from problem agendas in multiple respects. First, Shapere articulates domains in terms of immature and mature sciences,[86] which keeps rationality and scientific progress at the forefront of its motivations. This fits with attempts to offer general methodological rationale for theory choice, such as the appropriate 'type' of theory for ordered versus unordered domains (Nickles 1977), and differs from the emphasis in problem agendas on the concrete criteria of explanatory adequacy for a particular problem agenda and their stability across different theoretical frameworks, mature or immature. The observation that domains are intimately connected with theoretical frameworks and change frequently is also at odds with problem agendas (Nickles 1977; Shapere 1984b; cf. Nickles 1980, 1981). Second, Shapere does

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[86] "Although in more primitive stages of science (or, perhaps better, of what will become a science), obvious sensory similarities or general presuppositions usually determine whether certain items of experience will be considered as forming a body or domain, this is less and less true as science progresses (or, one might say, as it becomes more unambiguously scientific). As part of the growing sophistication of science, such associations of items are subjected to criticism, and often are revised on the basis of considerations that are far from obvious and naïve. Differences which seemed to distinguish items from one another are concluded to be superficial; similarities which were previously unrecognized or, if recognized, considered superficial, become fundamental" (Shapere 1977, 521).

not offer conditions of individuation for domains, which was a major component of our analysis of problem agendas.[87] Third, he explicitly includes techniques in his definition of domains (Shapere 1984b), something excluded from problem agendas. Finally, Shapere's discussion of domains is somewhat vague and it is not clear whether domains are to be understood as abstractions or linguistic entities, or something else (Nickles 1977).

The second relevant unit is Darden and Maull's idea of a 'field', which is discussed in several publications (Bechtel 1984, 1986b, 1993; Darden 1986, 1991; Darden and Maull 1977). The notion of a 'field' includes

> a central problem, a domain consisting of items taken to be facts related to that problem, general explanatory factors and goals providing expectations as to how the problem is to be solved, techniques and methods, and, sometimes, but not always, concepts, laws and theories which are related to the problem and which attempt to realize the explanatory goals" (Darden and Maull 1977, 44; cf. Maull 1977, 148).[88]

Darden has used this notion perspicaciously in her study of early 20th century Mendelian genetics where the existence of inter-field theories about genes and their behavior between several different disciplines/fields (cytology, transmission genetics, biochemistry) led to discernable theory change (Darden 1991). Two primary motivations for the construction of inter-field theories are a shared commitment to explaining different aspects of the same natural or experimental phenomena and a recognition that answering questions about these phenomena requires conceptual resources or techniques not available with a single field (Darden and Maull 1977, 49-50). Maull has emphasized the importance of negotiating special vocabulary between

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[87] "Our purpose here being the analysis of the concept of "theory," we will take for granted the *existence* of such bodies of information, and concern ourselves primarily with the generation of their problematic character, with a view to understanding how problems arise which require "theories" as their answers" (Shapere 1977, 526). "My primary concern … is with certain aspects of the second of these questions – the question of the ways in which items of a domain are described – and to a lesser extent with the first – the question of the ways in which scientific domains are marked out" (Shapere 1984b, 322).

[88] The domain referred to in this description is supposed to be Shapere's 'domain'. Darden and Maull were students of Shapere at the University of Chicago.

fields, not because meaning differences are critical but because terms are associated with concepts relevant for addressing distinct but related problems from the perspective of different fields (Maull 1977).

Several differences exist between fields and problem agendas. First, problem agendas are a more circumscribed unit of analysis in contrast to a ‘field’, which fits within approaches favoring ‘larger scale units’ (Bechtel 1993). Focusing on problem agendas allows one to explain why some of these other features might be included within a field (or discipline), as well as allowing one to assess interesting differences in explanatory expectations and methodology between investigative communities that share a common problem. In connection with this, problem agendas are decoupled from the methodological resources and techniques (‘formal and laboratory techniques’) used to solve them and can survive the demise of lines of research originally thought promising for dealing with the problem agenda. They are therefore more stable across historical periods of time (and thus historiographically useful) and also indicate how a particular field or discipline can deal with *multiple* problem agendas simultaneously. Also, there is no account of problem individuation from the field perspective because the *explanandum* is the coming together of fields using particular methodological resources to develop interfield theories rather than the coexistence of multiple problem agendas that demand different interfield configurations depending on which problem agenda is in focus.[89] In Darden and Maull’s discussion, problems are taken as relatively well defined and their explanatory burden as understood by researchers in different fields. Finally, because of this, there is no attention to how dissent from the need for an inter-level theory involving multiple fields might arise. The account of problem agendas has the dual resources of presupposition and theoretical

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[89] “In this paper we discuss fields that are within the broader scientific areas of biology and chemistry, but we do not give criteria for distinguishing more inclusive from less inclusive categories” (Darden and Maull 1977, 46).

constraint, which simultaneously sheds light on the rejection of an explanatory project and the conditions of problem agenda individuation in the midst of competing explanatory frameworks.

Concomitant with a focus on different units of analysis such as problems, domains, or fields, philosophers of science interested in issues pertaining to non-semantic incommensurability have used different relations between these units. Most discussions of theories have used the relation of 'reduction' to comprehend the dynamics between successor theories and their antecedents. Multiple difficulties have emerged from these analyses, including: (1) there is no accepted account of what theories are; (2) there is a rarity of successful reduction executions; (3) biology and other non-physical science disciplines do not have 'theories' in the desired sense(s); (4) reduction attempts require reifying theoretical frameworks, capturing their apparent essence while ignoring heterogeneity and variation among scientific practitioners; (5) there is an implicit assumption of progress involved ('*From* old theory *to* new theory'); and, (6) there is a tactical commitment to pair-wise comparisons. Sophisticated accounts of reductionism within the life sciences are able to meet some of these difficulties (Schaffner 1993a, 1993b) but remain strained in the evaluation of most philosophers of biology, ultimately missing critical components of the epistemic practices of biologists (Bechtel 1993; Burian 1993b; Darden 1996).

When different units of analysis are utilized (such as concepts, disciplines, fields, problems, methodologies, or criteria of explanatory adequacy), different types of relations are often invoked, including integration, unification, coordination, and synthesis, as well as fragmentation, disunity, and disintegration (Bechtel 1984, 1986b, 1993; Bunge 2003; Burian 1993b; Darden 1991; Darden and Maull 1977; Love 2003a; Maull 1977; Mitchell *et al.* 1997; Van Der Steen 1993). One can also continue to use the unit of theories while adopting different relations (cf. Darden 1991; Darden and Maull 1977), as well as using the relation of reduction with respect to different units (e.g. reducing one problem to another) (Nickles 1976). The units of analysis being developed here are conceptual clusters and problem agendas. The relations of importance are *integration* with respect to explanations offered for natural phenomena that compose problem agendas and *synthesis* with respect to the conceptual clusters utilized from different disciplines to offer integrated explanations (discussed further in Chapter 6).[90] This chapter articulates how a shared conception of the problem agenda is a critical first step in establishing shared criteria of explanatory adequacy across different disciplines that then motivates integrated explanations utilizing disparate methodologies and differing conceptual resources.[91]

2.4.3. Incommensurability, 'Values' in Science, and 'Standards' in Special Sciences

A continuous thread in this and the previous chapter is that the issues facing Evo-devo *qua* disciplinary synthesis in attempting to explain the origin of innovations and novelties bear important similarities to discussions of incommensurability that highlight differences in standards, aims, methodology, problems, or criteria of explanatory adequacy rather than meaning *per se* (a semantic interpretation of incommensurability). One way discussions of these issues emerged in the late 1970s was in terms of the nature of 'values' in scientific practice (Hempel 2001 [1983]; McMullin 1983). Because distinct investigative communities could arrive at an

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[90] Van der Steen has distinguished peripheral integrations, which do not concern the cores of theoretical structures, from substantive integrations, which do concern the central aspects of theoretical structures (Van Der Steen 1993). When I discuss integrated explanations, I mean explanations where substantive contributions are made from different disciplines undergoing synthesis.

[91] Evo-devo is referred to as a distinct 'discipline' (Hall 1999a; Raff 2000), and there are institutional reasons to consider it as such (professional societies, new research journals, dedicated funding, textbooks, and specified job openings) (Lenoir 1997; Messer-Davidow, Shumway and Sylvan 1993), but it seems better characterized as a cross disciplinary research cluster (Bechtel 1986b, 1993) when considering integrated explanations for natural phenomena, since they consist of multiple contributions from different existing disciplines to a purported common problem without researchers abandoning their extant disciplinary identity (see Section 6.5.3).

impasse based on differences in methodology or criteria of explanatory adequacy, a concern about the rationality of choosing between these research programs exercised philosophers of science. These analyses attempted to describe in scientific practice or philosophically explicate norms that applied to *any* scientific endeavor in order to isolate rationally binding criteria for choosing one or the other of the competing sets of values.

Although this discussion has mushroomed and become a rich area of philosophy of science research in its own right (Machamer and Wolters 2004), the aim of the present chapter is distinguishable from that of the discussions surrounding values in science. The germ of this difference was sown in chapter 1 when we identified the ‘middle range’ norms in view for the present study, which are intended to have binding force across several disciplinary communities but not necessarily be applicable to all of scientific research. More specifically, the goal was to make criteria of explanatory adequacy for evolutionary innovations and novelties explicit across the different disciplines supposedly relevant to Evo-devo. Articulating explanatory standards in an area of special science is methodologically distinct from articulating values operative in all of science, particularly with respect to the abstraction at which the values are postulated (cf. Shapere 1984a; Suppes 1990). This distinctness corresponds to the goal of offering concrete criteria applicable to the problem agenda under consideration for ongoing scientific practice rather than providing general methodological prescriptions for theory choice (Section 2.4.1, above). The standard set of epistemic values, such as predictive accuracy, internal coherence, consilience, fecundity, and simplicity, are much less concrete than the demand to attend to the form and function or the level of biological hierarchy in the problem agenda of evolutionary innovation and novelty. This abstraction has been a frustration to general accounts of these values because counterexamples seem to be easily found across scientific domains.[92]

But at the same time, there are clearly points of contact. The 'degree of generality' dimension detailed above is similar to the issue of theoretical scope. Even so, the former has a much less abstract connotation than the latter and does not require that a general account of scope be offered. This is why articulated explanatory standards for special sciences often have more precise import for making methodological decisions within these scientific disciplines. The main issue is not how to choose between one research program in molecular developmental genetics and another in functional morphology, both focused on explaining evolutionary innovations and novelties. Rather, the difficulty lies with appropriately bringing these two disciplines (and others) together to produce an integrated explanation, which is highlighted by specific attention to the characteristics of the problem agenda. Understanding the relationship between epistemic values in science and explanatory standards in special sciences requires further investigation, but it should now be clear which one is in view here and how they differ.

2.5. Recapitulation

We initiated our discussion in this chapter with a chain of arguments in favor of problems as units of analysis in philosophy of science. In order to have tools for assessing whether or not explaining the origin of evolutionary innovations and novelties constituted a distinct problem in biological research, we developed the notion of a problem agenda as sets of natural or

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[92] The distinction between formal versus material aspects of conceptual clusters is relevant here because the aim of articulating epistemic values in science emphasizes the form of theories or explanatory frameworks rather than their material structure or content, which is in view when articulating criteria of explanatory adequacy for special science problem agendas. "Desiderata of the kind we have considered have the character of epistemological norms or values. *They do not enter into the content of scientific theories*, but they serve as standards of acceptability or preferability for such theories" (Hempel 2001 [1983], 388 – my emphasis; cf. Shapere 1984a).

experimental phenomena that pose multiple intertwined research questions. Using resources from Aristotle's *Posterior Analytics* and van Fraassen's pragmatic theory of explanation in terms of answers to why-questions, we added structural depth to what components need to be isolated in a problem agenda. Presuppositions (acceptance of a need to explain phenomena) and theoretical constraints (shared conceptual features that allow the individuation of a problem agenda) were distinguished in order to facilitate cross-disciplinary explications of the criteria of explanatory adequacy for a problem agenda. Two features emerged as particularly relevant. First, because of the existence of many problem agendas that might be active in a particular research program, a key issue is distinguishing one problem agenda from another, which dovetailed with concerns about the distinctness of evolutionary innovations and novelties. Second, because individuation is accomplished by 'weak' shared theoretical constraints, problem agendas need to be explicitly characterized in order to fully limn their explanatory burden.

In Section 2.3 the problem agenda of evolutionary innovation and novelty was separated from the problem agenda of adaptation using both historical and philosophical rationale. The philosophical rationale emerged from the use of the tripartite conditions necessary for the operation of natural selection and led us to identify the problem agenda of innovation and novelty as being concerned with the origin of variation at particular phylogenetic junctures. This distinction was achieved without appeal to the reasons previously offered by biologists in favor of keeping innovation and novelty a separate problem. Next we proceeded to characterize the problem agenda in terms of three basic dimensions: form and function, level of biological hierarchy, and degree of generality. Each of these aspects helps make explicit what the criteria of explanatory adequacy are for Evo-devo researchers, including important terminological distinctions between innovation (function) and novelty (form) that emphasize the importance of character origination and the existence of the molecular paradox that highlights the non-transitivity of generality achieved from molecular level analyses.

Finally, problem agendas were situated in the larger philosophy of science literature on problems. Analyses of problems offered by other philosophers of science to capture the nature of scientific reasoning differ from problem agendas in several respects. Problem agendas are composed of multiple ‘problems’ and do not have the unit-structure assumed by many philosophers such as Toulmin and Laudan. They have conceptual depth in terms of their component problem diversity rather than as a consequence of being a particular type of problem and are more stable since they are not as distinctly anchored in particular theoretical frameworks because of their association with more stable natural phenomena. Problem agendas also differ from ‘domains’ and ‘fields’ because of the exclusion of methodological resources and focus on individuation from other problem agendas, as well as the historical stability of problem agendas. Despite these differences, problem agendas focus on relations other than reduction (such as integration) among units of analysis that have also arisen in these analyses of problems, domains, and fields. The aim of making criteria of explanatory adequacy explicit that motivated the development of the problem agenda tool was contrasted with discussions of values in science. An importance difference was identified between offering general methodological principles of theory choice and the attempt to elucidating concrete explanatory burdens of problem agendas in order to facilitate multidisciplinary research by addressing issues associated with non-semantic incommensurability.

3. AVIAN ILLUSTRATIONS: THE ORIGINS OF FEATHERS AND FLIGHT

3.1. Introduction

The purpose of this chapter is to provide concrete examples of the abstract distinctions set out in the previous chapter concerning the individuation and characterization of the problem agenda of innovation and novelty. To that end I have taken an extended case study from avian biology, the origin of feathers and flight, with the aim of illustrating how the language developed in Chapter 2 is applicable to and illuminating for ongoing research (cf. Suppes 1990). Using problem agendas as analytical units organizes existing research and allows explicit comparisons with the criteria of explanatory adequacy. This indicates what kind of a contribution is needed from different disciplines to offer an adequate explanatory framework, the self-proclaimed goal of Evo-devo proponents. Setting these concrete empirical issues within (1) form versus function, (2) level of biological hierarchy, and (3) degree of generality is of value to future research endeavors because it highlights what is required to adequately address the explanatory burden associated with the evolutionary origin of these avian features.

"Three questions lie at the heart of the debate about the evolution of birds: the origin of the group itself, the origin of feathers, and the origin of flight" (Prum 2003, 323). The depth of the literature on these three questions permits sufficient exploration of varying viewpoints but simultaneously prohibits a genuinely comprehensive treatment (cf. Padian and Chiappe 1998; Sereno 1999; Witmer 2002). First we need to restrict our attention to two of these questions because the origin of birds as a taxonomic group or category formally falls under the domain of the problem agenda of classification addressed by theories of systematics (Clark, Norell and Makovicky 2002; Dodson 2000; Padian 2001b; Padian and Chiappe 1998; Witmer 2002), also informed by paleontological evidence (Chiappe and Witmer 2002; Clarke *et al.* 2005; Currie *et al.* 2004; Forster *et al.* 1998; Hou *et al.* 1996; Melchor, de Valais and Genise 2002; Norell and Clarke 2001; Wright 2004; Xu *et al.* 2002; Zhou and Zhang 2002). Instructively, problems of classification were intertwined in earlier studies of avian innovations and novelties such that they were often referred to under the phrase 'the origin of higher taxa' (Bock 1965; Tucker 1938; see Chapter 4 for discussion). Owing to the analysis of Chapter 2, we now have the conceptual tools to follow the recommendation of Mayr to separate the origin of taxonomic groups from the origin of features of those groups identified as innovations or novelties (Mayr 1960). Only the latter two questions in Prum's triad (the origin of feathers and flight) fall within the domain of the problem agenda of innovation and novelty.[93]

This is not to say that a phylogenetic context can be ignored. Avian feathers and flight origination sit as research questions within the problem agenda of innovation and novelty, which demands attention to states of variation at specific phylogenetic junctures (Padian 2001a; Sumida and Brochu 2000). Understanding the origin of variation at these particular phylogenetic junctures will involve paleontological finds and phylogenetic reconstruction of known taxa. Therefore, we will need to consider disciplinary contributions from systematics and paleontology, in addition to those from developmental biology.

A second restriction involves issues that will not be discussed here. A growing literature exists on embryology and the tricky relationship of homology between avian and theropod

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[93] "The origin of a group, the origin of a structure, and the origin of a behavior or function are fundamentally different questions, and a cladogram primarily addresses the first" (Sumida and Brochu 2000, 494).

dinosaur digits (Burke and Feduccia 1997; Galis, Kundrát and Metz 2005; Galis, Kundrát and Sinervo 2003; Kundrát *et al.* 2002; Larsson and Wagner 2002; Vargas and Fallon 2005a, 2005b; Wagner and Gauthier 1999; Welten *et al.* 2005). It will be discussed only in so far as it is relevant to the interpretation of data for reconstructing the phylogeny of these taxa (cf. Feduccia 1999). There are also numerous papers on the bone histology of birds, dinosaurs, and mammals related to differences in post-natal growth (Case 1978; Chinsamy and Elzanowski 2001; Erickson *et al.* 2004; Erickson, Rogers and Yerby 2001; Horner, Padian and de Ricqlès 2001; Padian, de Ricqlès and Horner 2001; Rensberger and Watabe 2000). These results will only be mentioned regarding metabolic differences potentially connected with the origin of flight.

In order to provide orientation, let us anticipate some of the argument using the three characteristic dimensions of the problem agenda of innovation and novelty. First, feathers compose a form domain and flight that of function. Feathers are properly referred to as a novelty, a new structure in the history of life, while flight is accurately termed an innovation, a distinctive (though not exclusive) function of birds, later lost in some lineages. Although form and function can be conceptually separated, they ultimately must be integrated into organismal characters for an adequate analysis. What then are the apomorphic characters whose origins are the targets of these two explanatory projects? As will become clear below, this critical question does not have a univocal answer. Second, consider the level of biological organization. Both flight and feathers lie high up in biological hierarchies, composed of either numerous sub-functions (muscular movements, nerve coordination, and metabolic requirements) or structural components (shafts, barbs, cells, organelles, etc.). Compositional and procedural hierarchies will need to be identified, and whether they are being treated with respect to (developmental) space or (evolutionary) time. Finally, for generalization, we can ascertain the generality of any results and the applicability of other investigations to these particular cases, as well as any impact of the molecular paradox. The value of separating form from function will be evident as the domains of generalization for analyses of flight and feathers are highly divergent.

In order to make the connections transparent between the abstract discussion in Chapter 2 and these biological details, the research related to the origin of feathers and flight is reviewed using questions drawn directly from the main points argued for in my discussion of the problem agenda of innovation and novelty.

1. What is the *explanandum* phenomenon? How is the origin of the feature a qualitative departure from an ancestral condition?

2. What is the particular phylogenetic juncture under consideration for this feature? What is the disciplinary contribution of systematics?

3. What is the contribution of paleontology for understanding the kinds of variation available at the phylogenetic juncture in question?

4. How is there a discrepancy between states of variation past and present? What is the contribution of ontogenetic studies to understanding the developmental accessibility between ancestor and descendant genotype-phenotype relations?

5. How does the application of the distinctions between form, function, and character bear on analyzing the origin of this feature? What is the disciplinary contribution of morphological investigation?

6. How does the recognition of distinct levels of biological organization apply to the origin of this feature? Can we distinguish pertinent compositional and procedural hierarchies, either developmentally (spatially) or evolutionarily (temporally)?

7. How does the issue of generality apply to the origin of the feature? How does the molecular paradox apply and what explanatory principles are available or relevant?

8. What major research questions are associated with the origin of this feature? What kinds of solutions have been offered?

I close the chapter by drawing attention to some of the distinct advantages of conceptualizing specific explanatory problems, such as the origin of avian feathers and flight, through the lens of the abstract problem agenda of evolutionary innovation and novelty.

3.2. Explaining the Origin of Avian Form: Feathers

3.2.1.1. What is the *explanandum* phenomenon?

Although it is tempting to simply identify the target of explanation as 'avian feathers', this does not capture the explanatory target with appropriate precision. Birds can have as many as six basic types of feathers: (1) large, stiff remiges and rectrices along the posterior edges of the wings and tail (often referred to as flight feathers); (2) moderately sized contour feathers that cover the body; (3) small, 'fluffy' down feathers (natal or adult, the latter referred to as plumules); (4) semiplume feathers that are a distinct grade between contour and down feathers; (5) hair-like filoplumes; and (6) tiny facial bristles (Lucas and Stettenheim 1972a, ch. 5; Stettenheim 2000). All of these feather types vary in size, color, and/or shape. Using the contour feather for illustration, the parts of a typical feather include the shaft (quill), vanes along the shaft, and an afterfeather on the undersurface. The shaft is composed of the calamus (barrel), which is a short, circular tube anchored in the feather follicle, and the rachis, which is the solid shaft above the epidermis. The vane is a collection of branches (barbs) coming off of the rachis. The barbs (or ramus) then have smaller barbules emerge from them that overlay one another in different mesh-like patterns, which allows the vane to be distinguished into two domains: pennaceous and plumulaceous. The tight interlocking meshwork of pennaceous vanes, within and across feathers, is critical for their use in flight feathers. The afterfeather is an independent feather-like unit or collection of barbs attached near the base of the rachis. Although a contour feather includes all of these parts, remiges and rectrices have only pennaceous vanes whereas semiplumes and down feather are entirely plumulaceous. Anatomical and microstructural analysis reveals other differences not discussed here (Lucas and Stettenheim 1972a, ch. 5).

In addition to the different kinds of extant feathers and their component parts, there is also the issue of feather *grouping*. Feathers do not appear in an isolated fashion but are grouped into tracts as part of the integument or ‘skin’. These tract or plumage patterns, of which over fifty different kinds can be identified and grouped into eight major domains (Capital, Spinal, Caudal, Ventral, Lateral Body, Anterior Appendage, Posterior Appendage, and Powder Down Patches), are referred to as ‘pterylosis’ (Lucas and Stettenheim 1972a, ch. 2; cf. Mayerson and Fallon 1985). Feathers cover most of the body except for the feet, beak, and eyes (except in some ratites, such as ostriches or rheas, which have a naked head region).

Thus, the *explanandum* phenomenon is not as straightforward as might appear. The goal is to explain the origin of ancestral feathers or protofeathers that could have served as a basis for the diversification of feather types in particular feather tract patterns within the integument (Bartels 2003). Not surprisingly, there is a diversity of opinions about the nature of this ancestral feather morphology (Bock 2000; Brush 1996; Lucas and Stettenheim 1972a; Regal 1975). Explaining this origin requires comparison with the character state from which it was derived.

3.2.1.2. How is the origin of the feature a qualitative departure from an ancestral condition?

The origin of a protofeather is considered an evolutionary novelty if it is a qualitative departure from the ancestral condition. The operational identification of this departure for a structure is the criterion of non-homology.

> A morphological *novelty* is a structure that is neither homologous to any structure in the ancestral species nor homonomous to other structures of the same organism (Müller and Wagner 1991, 243, my emphasis).

The presumed ancestral integumentary condition for archosaurs is scales. Although birds have reticulate scales that can be homologized to archosaurian scales, some researchers are only willing to homologize the epidermal placode of scales and feathers (Harris, Fallon and Prum 2002; Prum and Brush 2002). Homology obtains at lower levels of organization but not for the mature scale and feather morphologies. Regardless of which ‘kind’ of feather was the first to evolutionary originate, or even if a ‘stem-group’ feather or integument is invoked (Bartels 2003; Budd 2001a; Schweitzer 2001), disagreement regarding relationships of homology between mature archosaurian scales and feathers flags the explanatory issue as concerning the problem agenda of innovation and novelty. The presupposition is that feathers are genuine evolutionary novelties, distinct from ‘microevolutionary’ phenomena such as variations in the scale morphology observed in the diversity of extant reptilian and avian integumentary structures.

3.2.2. What is the particular phylogenetic juncture under consideration for this feature? What is the disciplinary contribution of systematics?

Within current systematics, the overwhelmingly favored hypothesis for the origin of avian taxa is descent from a theropod dinosaur lineage (Chatterjee 1997; Clark, Norell and Makovicky 2002; Padian 2001b; Padian and Chiappe 1998; Paul 2002; Sereno 1999; Sumida and

Brochu 2000; Witmer 2002). Dissent from this hypothesis is still identifiable, with some researchers arguing for bird origination from a 'thecodont' archosauromorph (Feduccia 1996, 1999; Jones *et al.* 2000b). One difficulty cited for theropod ancestry is the discrepancy between digits in the forelimb of birds and theropods, the former having 2, 3, and 4 of the original pentadactyl limb based on embryological evidence, whereas theropods have 1, 2, and 3 based on paleontological analyses (cf. Burke and Feduccia 1997; Galis, Kundrát and Metz 2005; Galis, Kundrát and Sinervo 2003; Kundrát *et al.* 2002; Larsson and Wagner 2002; Vargas and Fallon 2005a, 2005b; Wagner and Gauthier 1999; Welten *et al.* 2005). Another putative difficulty is the temporal gap between these theropods found primarily in the middle to late Cretaceous and the origination of the avian clade, which most likely occurred in the early to middle Jurassic based on the late Jurassic morphology of *Archaeopteryx*. The timing difficulty is not as problematic as has been claimed since recent fossil finds occur earlier in the Cretaceous (Brochu and Norell 2001; Witmer 2002) and cladistic methodology does not demand that any of the most closely related taxa actually be ancestral to the avian clade (only sister groups) (Brochu and Norell 2001; Clark, Norell and Makovicky 2002; Padian 2001b; Padian and Chiappe 1998; Sumida and Brochu 2000). Some researchers have also suggested that differences in lung structure and ventilation militate against a theropod ancestry for birds (Ruben *et al.* 1997). Regardless, there is a robust set of synapomorphies that nests Aves within the theropod clade, such as foot and hind limb skeletal morphology, even though these do not disambiguate relationships among theropods themselves (Clark, Norell and Makovicky 2002; Holtz 2001). Avian behavior can now be attributed to theropod dinosaurs, such as nesting posture (Xu and Norell 2004).

Therefore, we are able to obtain a phylogenetic 'bounding' of the ancestral character state possibilities that contextualizes the transition from scale to 'feather'. Feathers originated within this theropod clade and thus the developmental transition under scrutiny likely occurred in one or more theropod dinosaur species. We cannot be content with the limited sister group claim identified by cladistic methodology because we are interested in an actual developmental transition from an ancestral lineage. The phylogenetic context for the origin of feathers is thus a hypothetical theropod common ancestor (or population thereof) that was extant most likely in the early Jurassic (Padian 2001b; Sumida and Brochu 2000).

3.2.3. What is the contribution of paleontology for understanding the kinds of variation available at the phylogenetic juncture in question?

Although *Archaeopteryx* has been at the center of most discussions regarding the origin of feathers (cf. Feduccia 1996; Wellnhofer 2004; Witmer 2002), many paleontological contributions have emerged in the past decade from ideal preservation conditions found in Chinese fossil beds (Zhou, Barrett and Hilton 2003). A number of these recent discoveries center on theropod dinosaurs that exhibit some kind of protofeather or feather morphology. *Caudipteryx* has symmetrical remiges and rectrices and *Protarchaeopteryx* has symmetrical rectrices (Qiang *et al.* 1998). Both have semi-plumes and down-like feathers all over their periphery, suggestive of insulation. *Sinosauropteryx* has plumules resembling those of modern birds (Chen, Dong and Zhen 1998). These integumentary structures are epidermally located, in the same topological position as feathers, and share morphological features of filaments, making the judgment of homology with modern feathers fairly robust (Padian, Qiang and Shu-An 2001).

The dromaeosaurid *Sinornithosaurus* has integumentary filaments that are more difficult to interpret (Xu, Wang and Wu 1999) but further study has shown multiple filaments in association, implying homology with avian feathers, like those of *Caudipteryx* (Xu, Zhou and

Prum 2001). Morphologically similar integumentary filaments are observable on basal tyrannosauroids (Xu *et al.* 2004) and *Beipiaosaurus*, a therizinosauroid, has integumentary filaments similar to *Sinosauropteryx* (Xu, Tang and Wang 1999). Another theropod, *Microraptor*, has both plumulaceous and pennaceous feathers, some with asymmetrical vanes akin to flight feathers (Xu 2000; Xu *et al.* 2003). Filamentous impressions associated with theropod tracks in the lower Jurassic have recently been put forward as the earliest known filaments, pre-dating *Archaeopteryx* by 50 million years (Kundrát 2004).

Debates remain about these integumentary structures, although more recent finds make it highly unlikely that they are muscle fibers, flayed collagen, or the integumentary filaments of secondarily flightless 'birds' (Martin and Czerkas 2000; Ruben and Jones 2000; cf. Paul 2002).[94] Despite the difficulty of interpreting these features, close approximations to modern feather morphology (pinnate feathers with a rachis and barbs) have now been identified in dromaeosaurids (Norell *et al.* 2002), as well as oviraptosaurids (*Caudipteryx*) and coleurosaurs (*Protarchaeopteryx*). An outcome of these fossil finds is the recognition that feather-like integumentary filaments exhibited greater diversity than is observed for extant avian taxa (Schweitzer 2001). The filamentous integument of these various dinosaurs has been likened to prototypical versions of modern contour feathers (Xu, Zhou and Prum 2001). Ancestral avian forms (e.g. *Protopteryx*) from the Early Cretaceous period have three identifiable feather types: flight, down, and tail feathers (Zhang and Zhou 2000; cf. Zhang and Zhou 2004).[95] Most researchers concur that theropod dinosaurs had both 'protofeathers' and true feathers, and therefore the origin of feathers is not something that occurred only in the avian lineage, nor in

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[94] Some researchers caution against claims of homology between theropod integumentary filaments and feathers based on studies of feather-type β-keratin in non-feather integument of avian species, such as the beard of wild turkeys (Sawyer and Knapp 2003; Sawyer *et al.* 2003b; see discussion below in Section 3.2.4).

[95] Fossilized feathers are also found apart from organismal structures, which allows for their use in reconstructions of a temporal juncture but not a phylogenetic one (cf. Kellner 2002).

coordination with the function of flight (cf. Padian, Qiang and Shu-An 2001; Prum and Brush 2002; Witmer 2002). The diversity of transitional morphology observed in these filamentous integuments has been interpreted with developmental hypotheses on the origin of feathers (Ji *et al.* 2001; Kundrát 2004; Schweitzer 2001; Zhang and Zhou 2000; see below, Section 3.2.8).

Part of the debate surrounding these ‘feathers’ concerns their place in the geological record, related to the temporal gap objection to current systematic consensus on avian relationships with theropods. The feathers on theropod dinosaurs occur in the Cretaceous period while *Archaeopteryx*, unambiguously having feathers, is located in the late Jurassic. A fossil archosaur from the Triassic period has been claimed to have feathers structures (Jones *et al.* 2000b), thus pushing back the origination of feathers prior to the emergence of theropods. But the status of these epithelial appendages is unclear and many researchers argue that they are a form of modified dorsal scales (Prum *et al.* 2001; Reisz and Sues 2000). Other potentially relevant taxa have remained too controversial to be included in analyses, such as *Protoavis* (Chatterjee 1997; see Witmer 2001, 2002).

3.2.4. How is there a discrepancy between states of variation past and present? What is the contribution of ontogenetic studies to understanding the developmental accessibility between ancestor and descendant genotype-phenotype relations?

The basic embryological events surrounding feather formation have been extensively described elsewhere (cf. Bereiter-Hahn, Matoltsy and Richards 1986; Chuong 1993; Chuong *et al.* 2000; Chuong and Widelitz 1998; Davidson 1983a, 1983b; Lucas and Stettenheim 1972b, ch. 7; Mayerson and Fallon 1985; Sengel 1976; Stettenheim 2000; Wessells 1965; Yu *et al.* 2004). Taking contour feathers as an exemplar, without reference to normal stages for chick development, feathers begin forming through an inductive interaction between epidermis (ectoderm) and dermis (mesoderm). Feather primordia begin as mesenchymal condensations (dermis) underlying elongating epidermal cell clusters at particular foci (feather germs). Dermal cells increasingly congregate beneath these epidermal foci into a placode and then anchor filament bundles that extend from the epidermal-dermal interface down into dermis. Continued epidermal cell elongation is followed by elevation through rapid cell proliferation in the feather bud. Barb ridges form, follicle formation occurs at the base of the placode, muscles begin to orient around it in the dermis, and barb ridges begin to differentiate (barbules emerge from barb shafts, then barbules themselves branch into hooklets). Additional fine-scale differentiation occurs throughout the nascent feather structure from more distal to more proximal structures.[96] Subsequent and coordinate with morphological differentiation is a hardening of the feather structure (keratinization) and deposition of materials conferring color (melanin, carotenoids, and porphyrin pigments) (cf. Prum *et al.* 1999; Yu *et al.* 2004). Molting and regeneration of feathers occur post-embryonically throughout avian taxa (cf. Stettenheim 2000; Yu *et al.* 2004).

A number of different molecular components relevant to scale and feather morphogenesis have been isolated in the past fifteen years (cf. Chuong 1993; Chuong and Noveen 1999; Widelitz and Chuong 1998; Wu *et al.* 2004; Yu *et al.* 2004). Bone Morphogenetic Proteins (BMPs) and Protein Kinase C act as inhibitors of placode formation thereby contributing to the spacing of feather buds within a feather tract in contrast to feather bud activators such as *Sonic Hedgehog* (*Shh*), *Fibroblast growth factors* (FGFs), Protein Kinase A, TGF β2, *Follistatin*, and *Eph-A4* (Ashique, Fu and Richman 2002; Jung *et al.* 1998; Morgan *et al.* 1998; Nohno *et al.*

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[96] "A feather does not grow like a plant, by sending out braches and twigs, mostly at the periphery. Cell division occurs mostly at the base of the feather germ, and the parts differentiate as they move upward. Accordingly, the distal and peripheral parts of a growing feather are more fully developed than the proximal and central parts" (Lucas and Stettenheim 1972b, 351).

1995; Noramly and Morgan 1998; Noveen, Jiang and Chuong 1995, 1996; Patel, Makarenkova and Jung 1999; Scaal *et al.* 2002; Song, Wang and Goetinck 1996; Ting-Berreth and Chuong 1996a, 1996b; Widelitz *et al.* 1996). β-catenin plays a central role in the initiation of the epidermal placode, follicle formation, and primary formation of the feather bud (Noramly, Freeman and Morgan 1999; Widelitz *et al.* 2000). Low activity is detected in avian scale morphology with increased levels corresponding to the formation of feathers or hair (Widelitz *et al.* 2000). In response to β-catenin, genes from the Wnt signaling pathway are activated such as *Wnt-7a*, which is involved in anterior-posterior asymmetry of the feather, as well as its proximal-distal elongation (Widelitz *et al.* 1999; cf. Chang *et al.* 2004).

The molecular heterogeneity of the feather bud after induction of the epidermal placode and dermal condensation breaks out into three basic areas: (1) an anterior domain expressing *Msx-1*, *Msx-2*, and *Hox* genes; (2) a posterior domain expressing *FGFR-2*, *Wnt-7a*, *lunatic fringe*, *Delta-1*, and *Serrate-1*; and, (3) a middle domain expressing *Notch-1* and *Shh* (Chuong 1993; Chuong and Noveen 1999; Widelitz and Chuong 1998; Widelitz *et al.* 2003). Interaction among these proteins across domains is critical for maintaining the morphogenetic processes generating feather morphology (Widelitz *et al.* 1999). Some homeobox genes are expressed in gradients in both the mesoderm and ectoderm of feather buds (Chuong *et al.* 1990), while others are confined to the epithelium (Noveen *et al.* 1995). *Notch-1* and *Delta-1* are localized to the feather bud early on while *Notch-1* and *-2* and *Serrate-1* and *-2* are subsequently activated throughout the developing morphology of the feather (Crowe *et al.* 1998; Viallet *et al.* 1998). These genes are strongly associated with anterior-posterior axis formation and maintenance in the feather bud (Chen *et al.* 1997; cf. Chen and Chuong 2000).

Anterior-posterior expression patterns of *Shh* and the presence of *Bmp2/4* in feather and scale primordia are conserved but their interaction as a signaling module is redeployed in the patterning of barbs and rachis, which is involved in determining plumulaceous versus pennaceous vane structure (Harris, Fallon and Prum 2002). *Shh* is first expressed in the ectoderm after epidermal differentiation has begun and plays a causal role in forming the feather bud (Morgan *et al.* 1998; Nohno *et al.* 1995; Ting-Berreth and Chuong 1996b), as well as inducing apoptosis in later differentiation events (Ting-Berreth and Chuong 1996b; Yu *et al.* 2002). Antagonism between BMP4 and Noggin contribute to feather branching, where the former is involved in initiating rachis formation and fusion of barbs while the latter enhances the rachis and induces branching of barbs (Yu *et al.* 2002). TSC-22 is downstream of BMPs and receptor tyrosine kinase (RTK), and mediates these signals (Dohrmann *et al.* 2002), whereas *groucho-related gene* integrates input from the Wnt pathway within the placode (Houghton, Freeman and Morgan 2003). Nuclear oncogenes (e.g. *c-myb*) are active in domains of cell proliferation within regions of the feather bud (Desbiens *et al.* 1991; cf. Desbiens, Turque and Vandenbunder 1992). Other downstream components include the ectodysplasin pathway involved in follicle formation (Houghton, Lindon and Morgan 2004) and *cDermo* expressed in dermal condensations (Scaal *et al.* 2002).

In addition to regulatory genes, the structural gene family of keratins has been analyzed (cf. Rogers and Dunn 1998), as well as a variety of cell adhesion molecules (e.g. tenascin, integrins, NCAM). Cell adhesion molecules are critical for morphogenetic movements during ontogeny and their differential activation is involved in cell interactions during feather and scale morphogenesis (Chuong and Edelman 1985a, 1985b; Gallin *et al.* 1986; Jiang and Chuong 1992; Shames, Bade and Sawyer 1994; Shames, Jennings and Sawyer 1991). α and β keratins are critical structural component of scales, feathers, and hair (Bereiter-Hahn, Matoltsy and Richards 1986). Scutellate (rectangular) scales primarily contain β-keratin but reticulate scales have α-keratin. Although birds do have scales, they never intergrade with feathers (Stettenheim 2000). Among the β-keratins, a modified amino acid form is found in feathers (sometimes called ϕ-keratin) while other protein isoforms are in avian scales, claws, and beak tissues, as well as non-avian reptilian integuments (crocodile, turtle, lepidosaur) (Sawyer *et al.* 2000). Recently it was shown that feather-type β keratins are expressed in the beard of wild turkeys (Sawyer *et al.* 2003b), as well as in epidermal cell populations of avian scutate (round) scales (Sawyer *et al.* 2003a; cf. Sawyer and Knapp 2003). β keratin immunoreactivity has also been shown for at least one fossil taxon, the alvarezsaurid *Shuvuuia* (Schweitzer 2001; Schweitzer *et al.* 1999).

Less attention has been paid to epigenetic dynamics of feather development in comparison to molecular constituents. In part this is because morphogenesis and organogenesis are conceptualized in terms of underlying gene activation (Hogan 1999; Jung and Chuong 1998; Pispa and Thesleff 2003) and thus fewer experiments have been directed at understanding their potential significance. One study demonstrated that cells self-organize into a periodic pattern in feather primordia (Jiang *et al.* 1999). The location of feather primordia is not predetermined but results from mesenchymal cells aggregating in a random fashion (see below, Section 3.2.6). Subsequently a more robust model was offered, explicitly integrating genetic and epigenetic factors involved in feather formation (Jiang *et al.* 2004).[97] Mechanical forces in the functional microanatomy of integumentary musculature have been postulated to play a role in the

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[97] "The genetic control provides transcription and translational control of molecules. Specific sets of cell surface molecules and intra-cellular signaling are produced for particular cell types. The molecular information endows cells and their micro-environment with particular properties. Based on these properties, cells interact in accordance to physical-chemical rules, and there are competition, equilibrium, randomness, and stochastic events, at this cellular level. Epigenetic events appear to play important roles at the cellular level. The integument pattern we observe is the sum of these cell behaviors" (Jiang *et al.* 2004, 131-132).

arrangement of feather primordia (Homberger and De Silva 2003). The significance of epigenetic dynamics for feather formation is highlighted when the evolutionary trajectory is in view, since the genetic mechanisms observed in avian ontogeny today may be a secondary hardwiring of initially epigenetic dynamics due to properties of the physical materials in the epithelial tissues and their interactions (Newman 1998).

Although there is a wealth of knowledge about avian feather initiation and morphogenesis, much less is known about reptilian scales (cf. Alibardi 2003, 2004a; Bereiter-Hahn, Matoltsy and Richards 1986; Homberger and De Silva 2000; Maderson and Alibardi 2000; Regal 1975; Ruben and Jones 2000; Sengel 1976).[98] No non-avian archosaurian model organism is being routinely investigated from a developmental standpoint. A feature that has received much attention is the absence of follicles in reptilian scales. Avian scale development appears to differ from avian feather and mammalian hair development in terms of early signaling that establishes the follicle, such as increased β-catenin, Wnt, and Notch signaling and decreased BMP activity (Yu *et al.* 2004). Much of what we know about scales comes from studies of *avian*, not reptilian, scales (cf. Sawyer and Knapp 2003; Shames, Bade and Sawyer 1994; Shames, Jennings and Sawyer 1991; Tanaka and Kato 1983).

Recent histological, anatomical, and descriptive embryological work on reptilian integumentary structures in crocodilians (Alibardi and Thompson 2001, 2002), lepidosaurs (snakes, lizards, and the Tuatara) (Alibardi 1998, 1999, 2002a, 2002b; Alibardi and Maderson 2003; Alibardi and Thompson 1999b, 2003), and turtles (Alibardi and Thompson 1999a) reveals several features that could be pursued with molecular genetic methods. Scales emerge as rounded, symmetrical elevations without condensations and subsequently grow asymmetrically

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[98] "Developmental anatomical data are insufficient to discuss plausible intermediates between an ancestral, scaled, reptilian skin and appendage-bearing, avian skin" (Maderson and Alibardi 2000, 513).

to a degree of overlap in a similar fashion for different taxa. Differences in scale formation typically occur with respect to growth and keratinization subsequent to these conserved sequences (cf. Alibardi and Sawyer 2002). For example, even though reptilian scales contain both α- and β-keratins, the interaction between these two keratins in the epidermis differs, with the crocodilian pattern matching that of birds and differing from turtles and lepidosaurs (Alibardi and Thompson 2001, 2002). Also, key histological features present in the reptilian epidermis, such as keratohyalin granules, are absent in birds (Alibardi 2004b). Developmental genetic studies of some of these reptilian taxa are necessary for a better understanding of changes in the mapping relation between genotype and phenotype for the origin of feathers as a qualitative departure from the ancestral state of scales.

3.2.5. How does the application of the distinctions between form, function, and character bear on analyzing the origin of this feature? What is the disciplinary contribution of morphological investigation?

An analysis of the origin of a form feature such as feathers demands a complementary discussion of functional complements and potential biological characters (form/function complexes). The skin or integument is usually understood to be an organ that in concert with functions such as evaporation prevention has obvious biological roles (e.g. protection). It is structurally composed of two layers of tissue (epidermis and dermis = cutis), or, alternatively three layers of tissue (cutis and subcutis) (cf. Lucas and Stettenheim 1972b, ch. 9; Stettenheim 2000). Integuments exhibit a high degree of diversity in structure and function, such as in a cockatoo bill, horse hoof, rhinoceros horn, whale baleen, or turkey beard. Morphological analysis implies that these different integuments are unlikely to be homologous (Homberger

2001). This highlights different functional *capacities* of integuments (e.g. soft versus hard) that is immediately applicable to the case of feather origination (Wu *et al.* 2004).

A variety of possible functions for feather structure have been proposed, including thermoregulation (homoeothermic or heat shielding), appearance and visual signaling (including sexual display and species recognition), antimicrobial chemical defense, repelling water, physical protection against the environment, prey capture, structural support, and tactile sensation (Bereiter-Hahn, Matoltsy and Richards 1986; Bock 2000; Menon and Menon 2000; Padian, Qiang and Shu-An 2001; Prum *et al.* 1999; Regal 1975; Stettenheim 2000). Some putative functions for feathers can be combined with other functions. For example, insulation and behavior functions can be combined to argue that feathers were originally for thermoregulation of eggs on the nest, i.e. brooding (Hopp and Orsen 2004; Padian, Qiang and Shu-An 2001). These kinds of combinations show the difficulty with functional attribution, as the thermoregulatory role in this case is not retention for individual homoeothermic needs but rather the shedding of heat for the benefit of offspring. Epidermal lipids (secreted by sebokeratinocytes) can also play a role in thermoregulation, coloration, and chemical defense (Menon and Menon 2000). When focusing on thermoregulation (cf. Regal 1975), the arrangement of feathers into plumage is in view as individual feathers do not act as thermal regulators on their own (Bereiter-Hahn, Matoltsy and Richards 1986; Wolf and Walsberg 2000). Functional possibilities demand attention to feathers being organized into tracts with specific muscular attachments (Bock 2000; Homberger and De Silva 2000, 2003; Lucas and Stettenheim 1972b, ch. 8; Mayerson and Fallon 1985). Even the widely held view that early feathers were somehow involved in thermal regulation has been challenged by focusing on the possible ectothermic status of *Archaeopteryx* (Ruben and Jones 2000).

These considerations confront us with the possibility of feather multi-functionality. Whether in the performance of multiple activities in parallel or conjointly, it may be problematic to match a single function to feather structure. That is, it may be inappropriate to ask: "But what was the original function of feathers?" (Sumida and Brochu 2000). The most widely accepted phylogenetic context only rules out flight association (Padian and Chiappe 1998; Sereno 1999). But those disagreeing with the cladistic conclusion regarding avian taxa continue to analyze functional demands from flight that would bear on feather origination (Homberger and De Silva 2000, 2003; Tarsitano *et al.* 2000). A major implication of multi-functionality is the absence of a univocal answer to conceptualizing character origination in the case of feathers. Multiple decompositions of characters (form/function complexes) are possible, and thus multiple biological roles could be the target of selection. The inference of function *from* particular structures is problematic in part because of the issue of multi-functionality (Lauder 1995).

3.2.6. How does the recognition of distinct levels of biological organization apply to the origin of this feature? Can we distinguish pertinent compositional and procedural hierarchies, either developmentally (spatially) or evolutionarily (temporally)?

The description of feather morphology indicates that a number of different levels of organization are identifiable when thinking about feather origins. One way of parsing feather structure as a compositional hierarchy in space (developmentally) has already been offered (Brush 1996): (1) *Monomers*: *ϕ*-keratin (modified β-keratins); (2) *Microfilaments*: linear association of monomers; (3) *Fibers*: regular, oriented microfilaments; (4) *Morphological Parts*: fiber structures produced from follicle; (5) *Feather*: combination of morphological parts; (6) *Plumage*: ordered distribution of feathers. Another way of carving up the morphological hierarchy of feathers is to describe different levels of complexity (Chuong *et al.* 2000): (1) competent epithelium; (2) placode; (3) symmetric short bud; (4) asymmetrical short bud; (5) long bud; (6) feather follicle; (7) downy feathers; (8) plumulaceous feathers; (9) pennaceous feathers; and, (10) flight feathers. One advantage with this representation is the recognition of morphogenetic processes required to achieve a particular level. For example, induction is required to go from competent epithelium to a placode or invagination must occur to produce a feather follicle from a long bud. Another advantage is as a key to interpreting relationships of homology. Reptilian scales only match up to level (5), *Sinosauropteryx* seems to map onto (6), *Caudipteryx* and *Protarchaeopteryx* achieve level (8) and (9), while *Archaeopteryx* and early Cretaceous avian forms match level (10). The difficulty with this representation is that the levels are not necessarily connected developmentally or evolutionarily (something the authors recognize), and thus it is not clear how to apply it to an explanation of feather origination.

In addition to compositional hierarchies, procedural hierarchies in morphogenetic processes can also be identified. The overall establishment of feather tracts and morphology proceeds through the following stereotypical steps: (1) a competent field or macropattern of feather tracts is established; (2) feather primordia site determination or micropatterning takes place within these feather tracts; (3) feather primordia are then oriented along a proximal-distal axis; (4) cell proliferation begins in the elongation and growth of the feather bud; and, (5) the production of branched structures through differential growth and apoptosis yields distinctive feather morphology (Chuong *et al.* 2000; Chuong and Widelitz 1998). There exists within this morphogenetic sequence another procedural hierarchy related to step 2, feather primordia origination (Jiang *et al.* 1999).

1) Cells become competent to form feather primordia and a feather field is established

2) When a threshold of cell density is reached, the random collision of ‘adhesive’ cells (bearing NCAMs) allows for the formation of unstable microaggregates (3-5 cells)
3) Microaggregate formation leads to increased adhesion molecule concentration, allowing for microaggregates to increase in size or merge with one another
4) Once a microaggregate reaches a particular size, a molecular signal is initiated that suppresses neighboring regions from becoming feather primordia (i.e. interprimordia), which also stabilizes the microaggregate itself
5) Periodic patterns form over the entire field
6) Differential survival of microaggregates; some consolidate to become stable dermal condensations, other disappear
7) Dermal condensations signal to epithelium; when competent, the epithelium responds with the formation of the epithelial placode over the dermal condensation

Within the first procedural hierarchy identified, compositional hierarchical relationships (feather primordia are parts of feather tracts) are also present. Other developmental hierarchies relevant to feather origination have been identified (cf. Prum 1999; see below, Section 3.2.8).

Although it is clear that both compositional and procedural hierarchies are present in space (or developmentally) for feathers, the application of these to an evolutionary transition (i.e. hierarchy in time) is less clear. A core research question is whether the observation of hierarchical relationships in space also needed to occur in evolutionary time; i.e. are ontogenetic processes also a record of phylogenetic sequences (see below, Section 3.2.8)?

3.2.7. How does the issue of generality apply to the origin of the feature? How does the molecular paradox apply and what explanatory principles are available or relevant?

A key point of contact for studies of feather origination with respect to the dimension of generalization in the problem agenda of innovation and novelty is the molecular genetic study of mammalian hair formation (Botchkarev and Paus 2003; Rogers and Dunn 1998; Wu *et al.* 2004).

β-catenin and other components of Wnt signaling play central roles in the initiation, morphogenesis, and differentiation of hair follicles in mice (Andl *et al.* 2002; Dasgupta and Fuchs 1999; Huelsken *et al.* 2001; Kishimoto, Burgeson and Morgan 2000; Millar *et al.* 1999). *Shh* is essential for hair follicle morphogenesis, preventing the subsequent establishment of dermal papillae (Chiang *et al.* 1999; Mill *et al.* 2003; St-Jacques *et al.* 1998). The BMP antagonist Noggin and TGF-β2 stimulate the induction of hair follicles from the mesenchyme (Botchkarev *et al.* 1999; Foitzik *et al.* 1999). The study of TSC-22 in the feather bud (Dohrmann *et al.* 2002) was motivated by the observed expression of TSC-22 in murine hair follicles (Dohrmann, Belaoussoff and Raftery 1999). A similar rationale was followed to discover the role of the ectodysplasin pathway in feather ontogeny (Houghton, Lindon and Morgan 2004; Laurikkala *et al.* 2002). Since the morphology of feathers and hair are highly divergent, generally applicable explanatory principles are found in follicle formation (or *early* feather development) and use of key initiating molecules such as β-catenin, Wnts, and BMPs (Jamora *et al.* 2003; Widelitz and Chuong 1998; Widelitz *et al.* 2000; Wu *et al.* 2004).

A different source of generality can be derived from attention to mechanisms of patterning and morphogenesis of epithelial appendages (Chuong 1993, 1998; Chuong and Widelitz 1998; Newman 1994, 1998). In addition to hair, other epithelial appendages such as teeth are relevant (Pispa and Thesleff 2003). All of these share an initial induction stage between epithelium and mesenchyme, the formation of placodes, a morphogenesis stage involving cell proliferation and movement, and a differentiation stage where specific features of morphology arise out of structural gene expression and cell death. One feature shared by all epithelial appendages is the preliminary establishment of a field or region (feather tracts or dentition fields) prior to the initiation of the specific morphology (feathers and teeth). This movement from macropatterning to micropatterning is a shared procedural hierarchy in developmental space for these appendages (Chuong and Widelitz 1998; McCollum and Sharpe 2001; Miletich and Sharpe 2003). A final point of contact in this area is the idea of a molecular capacity for phenotypic diversity (Brush 2000; Chuong 1998; Prum and Brush 2002; Prum and Williamson 2001; Stettenheim 2000; Wu *et al.* 2004). Epithelial appendages are capable of producing a wide array of structures because of the flexibility of inductive interactions and short-range signaling in epithelial primordia within the integument (Chuong 1998).

Consideration of generality brings model organisms back to the fore. There is both variation within particular species, within different body regions (Dhouailly *et al.* 1998) and variation across species with respect to avian integumentary structures (Bartels 2003; Lucas and Stettenheim 1972a). Since the domestic chicken is primarily investigated molecularly, it is unclear whether these highly derived molecular genetic patterns appropriately represent the ancestral transition from one genotype-phenotype mapping to another. The absence of studies on archosaurs and different avian species is a gap in the project of understanding the origin of feathers primarily because of the molecular paradox. Even if many of the gene expression patterns are similar, this does not guarantee an understanding of the origination of the higher structural levels, as gene co-option and convergence or the dissociation of gene expression and morphology could have occurred. Without denser taxonomic sampling of these developmental events, the challenge from the molecular paradox cannot be adequately addressed.

A second application of the molecular paradox is observable in molecular genetic studies isolating β-catenin and Wnt signaling in common among the early events of feather and hair follicle formation. Although these studies are crucial and highly informative, they do not directly address the formation of specific feather morphology in contrast to that of hair (which has a very different higher level morphology). Histogenetic studies have also identified many similarities of early formation between feather and hair (Bereiter-Hahn, Matoltsy and Richards 1986; Sengel 1976) but less attention has been focused on later events surrounding differentiation that are responsible for the higher levels of organization within the feather structure (cf. Harris, Fallon and Prum 2002; Yu *et al.* 2002).

3.2.8. What major research questions are associated with the origin of this feature? What kinds of solutions have been offered?

Several distinct research questions can be identified for the origin of feathers.

a) What are the roles of genetic and epigenetic factors in different stages of feather formation? How do genetic factors operate in different stages of feather formation? How do epigenetic factors operate in different stages of feather formation?

b) What are the expression patterns for the many genes identified in feather ontogeny in non-avian reptilian systems? How much variability in expression is there during the ontogeny of scales and does it correlate with different scale morphologies?

c) Can denser taxonomic sampling allow us to reconstruct more precisely a hypothetical common ancestral integumentary state for the theropod lineage that gave rise to birds?

d) Can Jurassic feathered theropods be found? Are there any genuine feathered non-theropods?

e) Is there a way to test different multifunctional combinations for feathers? Can we rule out other initial functions besides flight or better support a ‘primary’ function?

f) How congruent are the compositional and procedural hierarchies observed in the development and morphology of extant feathers with their evolutionary origin?

g) To what degree can insights about feather morphogenesis be derived from studies of hair development? Is feather development in avian species besides *Gallus* identical? If not, what kind of variability exists and does it correlate with phylogenetic distance or is it clade specific?

More questions could be identified but these represent issues that arise from the different domains we have canvassed and also show the need for contributions from different disciplinary areas. The recognition of a need for interdisciplinary approaches is observable in several recent papers (Chuong and Homberger 2003; Chuong *et al.* 2003; Maderson and Homberger 2000; Prum 1999; Prum and Brush 2002; Wu *et al.* 2004).[99]

Partial solutions have been offered for the origination of feathers on different occasions and two different explanatory projects are reviewed here. The first is a model articulated primarily by Prum in light of developmental considerations and supported by paleontological finds in China (Prum 1999; Prum and Dyck 2003; Prum and Williamson 2001). A related model from Brush is built out of slightly different considerations including feather biochemistry (Brush 1996, 2000) but both authors have fused their account elsewhere (Prum and Brush 2002). The core component of this model is that feather origination pivots on the origination of a cylindrical follicle, rather than a transformation of the mature scale structure. This follicle would have produced an undifferentiated hollow cylinder (Stage I). Stage II involves the differentiation of the collar into barb ridges that mature into a set of unbranched barbs on an anchoring calamus.

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[99] "…interdisciplinary collaboration, drawing from different backgrounds, perspectives and approaches, has the greatest potential to bring together all the knowledge and tools that are needed for a comprehensive understanding of the biology of the integument" (Chuong and Homberger 2003, 7).

Stage IIIa involves helical displacement and the production of a pinnate feather with unbranched barbs fused to a central rachis. Stage IIIb pertains to the origin of barbules on the unbranched barbs. Stage IIIa or IIIb could have originated first but both are prerequisites for proceeding to the next stage. Combined (Stage IIIa+b) we get a bipinnate feather on a central rachis with barbules emergent from barbs on the rachis forming a pennaceous vane. Stage IV initiates asymmetrical differentiation of the barbules into hooklets giving a distinct proximal-distal orientation. A lateral displacement of the new barb locus (helical displacement in Stage IIIa) comprises Stage Va and leads to the production of an asymmetrical, closed pennaceous vane resembling modern rectrices and remiges. Alternatively (Stage Vb), an additional barb locus would allow for the production of a second pattern of helical displacement and thus an afterfeather. Other feather morphologies can be derived from variants on Stage V through different developmental transformations.

Prum claims this model is functionally neutral but it is more accurate to say that it allows for multi-functionality while excluding particular functions such as flight (at least initially). The most attractive aspects of this model are its consistency with the evidence from the fossil record (correlating particular stage morphologies with integumentary filaments on theropod dinosaurs), incorporation of developmental data and extant feather diversity (all stages correspond to something similar in existing morphologies and can be observed to occur developmentally), and that it explicitly attends to compositional and procedural hierarchies in time and space. Because of this latter component, the question of whether phylogeny matches ontogeny can be directly addressed (cf. Lucas and Stettenheim 1972b, 346). Even though plumulaceous feathers are hypothesized to be ancestral to pennaceous feathers, it is not because the first feathers to appear in extant birds are plumulaceous. Also, barb ridge formation (Stage II) occurs during feather ontogeny prior to the complete establishment of the follicle (Stage I). And yet in other cases a compositional hierarchy imposes a constraint on the procedural hierarchy. Barbule origination (Stage IIIb) is dependent on the prior existence of barbs (Stage II) in which they are morphologically anchored. One outstanding issue with respect to the model is how existing knowledge of the molecular developmental genetics of feather formation (Chuong *et al.* 2000; Chuong *et al.* 2003; Widelitz *et al.* 2003; Wu *et al.* 2004) fits within these stages.

The second explanatory model derives the origin of feather structures from certain functional strictures by transforming a scale into a feather (Maderson 1972; Maderson and Alibardi 2000; Regal 1975).[100] Regal argued from a study of lepidosaurian scales (from the lizard *Sceloporus*) that heat shielding initiated a transformation toward a feather via progressive enlargement and elongation (Regal 1975). Although intriguing it does not treat questions of the developmental production of these transformations or whether raised scales found in *Sceloporus* is an appropriate ancestral condition from which to model feather origins. Maderson and Alibardi have articulated a hypothesis of specialized protofeathers growing from the tips of archosaurian scales through heterochronic modulations of keratinocyte behavior, which helps explain the biased β-keratin content of feathers (Alibardi 2003, 2004a; Maderson 1972; Maderson and Alibardi 2000). A major difficulty for both Regal and Maderson/Alibardi is the transformation of a planar scale bud into a cylindrical follicle, the latter of which is given scant attention (cf. Maderson and Alibardi 2000, 526). Inadequacies of the models include inattention to a particular phylogenetic juncture informed by systematics and the developmental generation of feathers, as well as relying on controversial paleontological specimens (Jones *et al.* 2000b). They ignore key disciplinary contributions in an interdisciplinary explanatory enterprise.

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[100] "…the chief difficulty in thinking about the evolution of the first feathers is the difficulty in accounting for the genesis of the structure through a continuous sequence of selective forces and with a continuous series of hypothetical morphological steps that are functionally plausible" (Regal 1975, 35-36).

3.3. Explaining the Origin of Avian Function: Flight

3.3.1.1. What is the *explanandum* phenomenon?

As might be expected from our discussion of feathers, the *explanandum* phenomenon for the origin of flight is also not straightforward. Flight can be considered from the perspective of drifting/floating, jumping, and gliding in addition to the flap stroke of 'powered' flight that is usually recognized (Azuma 1992; cf. Norberg 1990a). Within gliding flight, at least five different modes can be distinguished: cruising, soaring, diving, bounding, and hovering (Azuma 1992). The goal is to explain the origin of an ancestral flying function in a lineage in which the function did not previously exist, that could have served as a basis for the diversification of observed differences in flying function today. It is (again) no surprise that there is a diversity of opinions about the nature of this ancestral flying function (Feduccia 1996; Norberg 1990a, ch. 13; Padian 1985; Padian and Chiappe 1998). Explaining this origin requires comparison with the character state from which it was derived.

3.3.1.2. How is the origin of the feature a qualitative departure from an ancestral condition?

Similar to our discussion of feathers, we begin to pick out flight as a qualitative departure from the ancestral condition via a criterion of non-homology.

> An organismal *innovation* is a function that is neither extant in the ancestral species/lineage nor operational elsewhere in the functional context of the same organism.

In this case, the ancestral lineage is assumed to not have the flying function, being somehow a terrestrially oriented animal with respect to locomotion. Many researchers define flight in terms of a powered flight stroke, which means that not having the flying function in the ancestral lineage is not being able to perform the flight stroke (Padian 1985, 1987; Rayner 1988). Assessing the ability to perform the activity of flight must be done indirectly through attention to skeletal and muscular morphology. Terrestrial modes of locomotion are also inferred from morphological features. The two basic ecological modes relevant to understanding the ancestral condition are arboreality (tree-dwelling) and cursoriality (ground-dwelling). Each of these implies the existence of certain morphological features (e.g. in the forelimb apparatus) that can be identified in extant and extinct taxa. The presupposition is that flight is a genuine evolutionary innovation and distinctly different from 'microevolutionary' phenomena, such as modifications of flight modes observed in the diversity of extant avian taxa.

3.3.2. What is the particular phylogenetic juncture under consideration for this feature? What is the disciplinary contribution of systematics?

All of the discussion in Section 3.2.2 is relevant for understanding the potential transition states of variation and will not be rehearsed. Much of the dispute regarding the use of cladistic methodology has been driven by a functional approach to the origin of flight: instead of moving from a phylogenetic reconstruction to a functional hypothesis, many researchers put forward a functional hypothesis and then search for phylogenetically relevant taxa (Feduccia 1996; cf. Padian and Chiappe 1998; Sumida and Brochu 2000; Witmer 2002). Assuming the former is a preferred methodology (Lauder 1981, 1990; Lauder 1995; Padian 1995; Witmer 2002), theropod dinosaurs are once again the appropriate phylogenetic juncture (Padian 2001a).[101] If we return to the phylogenetic context from 3.2.2, the major difference from the scoring of feathers is that *only*

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[101] An interesting twist on this consensus is the claim that theropods are secondarily flightless and thus have their 'bird-like' features by virtue of a shared common ancestral flying form (Paul 2002; cf. Jones *et al.* 2000a).

avian taxa have the function of flight. The dissociation of feather origination from flight origination is thus made more explicit.

This phylogenetic context would seem to favor cursorial hypotheses (Sumida and Brochu 2000) but these are not necessarily linked nor do arboreal hypotheses require non-theropod ancestry (Homberger and De Silva 2000; Padian 2001a; Rayner 1988; Witmer 2002; cf. Feduccia 1996). Knowledge of theropod anatomy does indicate that they were active, bipedal, ground dwelling carnivores and do not appear to have had the morphological features expected for climbing trees, i.e. scansorial adaptations (Padian 2001a; Padian and Chiappe 1998).

3.3.3. What is the contribution of paleontology for understanding the kinds of variation available at the phylogenetic juncture in question?

Many paleontological studies have concerned anatomical inferences to the activity of *Archaeopteryx*. Although much disagreement remains (cf. Feduccia 1996), a number of researchers think *Archaeopteryx* did not have limb morphology allowing it to perch (Padian and Chiappe 1998). Dromaeosaurids have the sideways-flexing wrist joint that is a prerequisite for the flapping of wings to produce thrust (Gauthier and Padian 1985; Gishlick 2001) and recent fossil finds within this group demonstrate the existence of appropriate shoulder girdle modifications that offer some support to a cursorial origin for avian flight via theropods (Xu, Wang and Wu 1999; cf. Middleton and Gatesy 2000). Other fossils, once set into a phylogenetic context, indicate that much of the skeletal morphology required for flight arose for other purposes among theropod dinosaurs, such as the hollowing of long bones, removal of a weight supporting role for pedal digit I, overall body size reduction, and expansion of the coracoid and sternum for increased attachment and number of pectoral muscles required for a flight stroke

(Norell and Clarke 2001; Padian and Chiappe 1998; Sereno 1999; Sereno and Chenggang 1992; Xu 2000). Some recent theropod fossil discoveries appear to have scansorial adaptations of skeletal morphology and therefore, potentially, occupied an arboreal habitat (Xu 2000; Xu *et al.* 2003). Paleontological evidence thus supports decoupling theropod ancestry from cursorial theories of flight origination.

Studies of morphology correlated with increased neuromuscular control demands of flight (cf. Goslow, Wilson and Poore 2000), such as the need for increased sensory integration, equilibrium maintenance, and coordination of suites of muscles, have recently been executed using techniques such as high resolution computerized tomographic (CT) scans. Avian skulls show a marked increase in cranial capacity over theropod dinosaurs (Marugán-Lobón and Buscalioni 2004; cf. Larsson 2001), the expansion of which may be related to nervous system requirements for flight control including larger eyes (Goslow, Wilson and Poore 2000). Detailed CT studies of *Archaeopteryx* also bear this out, indicating an enlarged forebrain with increased vision sensory capacity, as well as auditory and spatial perception associated with inner ear function (Domínguez Alonso *et al.* 2004).[102]

Histological analysis of bone in dinosaurs, birds, and other extinct and extant taxa sheds light on the origin of small size in the avian lineage. The slowing of growth rates at some or all of the different ontogenetic stages is correlated with small size in the theropod lineage, indicating that the origin of avian morphology capable of flight function was likely affected by this variable (Case 1978; Chinsamy and Elzanowski 2001; Erickson *et al.* 2004; Erickson, Rogers and Yerby 2001; Padian, de Ricqlès and Horner 2001; Rensberger and Watabe 2000). This may have had a consequent effect on metabolic rates, contributing to the achievement of physiological requirements on flight function (see below, Section 3.3.7).

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[102] The same morphological trends are also observable in pterosaurs (Witmer *et al.* 2003, see below, Section 3.3.7).

3.3.4. How is there a discrepancy between states of variation past and present? What is the contribution of ontogenetic studies to understanding the developmental accessibility between ancestor and descendant genotype-phenotype relations?

There is a glaring discrepancy of available developmental evidence between feather origination and flight origination studies. Relatively few investigations of the ontogeny of flight exist. In part this derives from the fact that flight emerges quite late during development, at a time when the kinds of molecular developmental genetic studies currently favored are not typically deployed. Post-natal avian development has been largely overlooked except in a few exceptional cases (Freeman and Vince 1974, ch. 8; O'Connor 1984; Starck and Ricklefs 1998a). Phylogenetic patterns in the evolution of avian development mode (altricial to precocial) need to be integrated with similar data from non-avian reptilian taxa (cf. Ricklefs and Starck 1998; Starck and Ricklefs 1998b). Attention needs to be given to neural, musculature, and sensory system ontogeny after hatching, as well as locomotive related behavior, the events of which have been studied less intensely than early embryogenesis (Düttman, Bergmann and Engländer 1998; Freeman and Vince 1974, 71-73, 84-103, 113-4; Hohtola and Visser 1998; O'Connor 1984; Starck 1993). Similar considerations apply for later developmental studies of reptilian taxa (turtles, crocodiles, and lepidosaurs).

The possibilities for this kind of research have been recently revealed in studies of wing-assisted incline running (WAIR) behavior in juvenile and adult birds (Bundle and Dial 2003; Dial 2000, 2003). By flapping wings during locomotion on an inclined substrate, increased hind limb traction is gained, a response usually observed when attempting to escape from predators. Without WAIR, 45º is the maximum angle achievable whereas with WAIR, hatchlings achieve

50º, 4 day-old birds 60º, 20 day-old birds vertical (90º) ascents, and mature birds can negotiate 105º overhangs (Bundle and Dial 2003; Dial 2003). These results allow for a different hypothesis concerning the origin of flight because the flapping motion of the forelimb functions in an aerodynamically beneficial manner prior to any departure from the ground. The relevance of ontogenetic studies to understanding the origin of flight are also indicated by the recognition that size reduction via heterochrony has occurred frequently in avian evolution (Chatterjee 1997; Chatterjee and Templin 2004; Feduccia 1996). Mechanistic investigations need to be undertaken in different reptilian and avian taxa to better understand the causes underlying these patterns of developmental timing alterations.

3.3.5. How does the application of the distinctions between form, function, and character bear on analyzing the origin of this feature? What is the disciplinary contribution of morphological investigation?

When considering natural complements to the function of flight, several structural features are immediately relevant: limitations on body weight, modifications of body morphology (trunk, wing, tail), skeleton (skull, teeth, pectoral girdle, wing), flight muscles, respiratory system, cardiovascular system, sensory modifications (sight) and brain capacity alterations (King and King 1979). Body mass affects take off performance with respect to muscle strain on the pectoralis (Tobalske and Dial 2000), which provides the depressing motion of the downstroke and protraction/retraction of the humerus in different flight modes (Dial and Biewener 1993; Dial *et al.* 1988; Williamson, Dial and Biewener 2001). The force production of muscles involved in flapping motion is subject to high degrees of variability (Tobalske and Dial 1994), as are air speeds (Rayner *et al.* 2001). Portions of the limb integument (such as the propatagium) are central to producing lift (Brown and Cogley 1996), whereas the supracoracoideus is involved in upstroke movement critical for takeoff (Poore, Sánchez-Haiman and Goslow 1997a, 1997b; Sokoloff *et al.* 2001). Tail muscles explicitly come into play during flight but are not active during walking locomotion (Gatesy and Dial 1993). Forearm muscles are required for take off and controlled landing but unnecessary for flapping flight (Dial 1992). The execution of the flight stroke has a direct impact on the respiratory system and their interaction is subtly coordinated (Boggs, Jenkins and Dial 1997; Boggs *et al.* 1997). In addition to specific morphological scaffolding for flight, in-flight behavioral strategies (e.g. wing beat kinematics and maneuvering) are also needed to execute this activity (Tobalske and Dial 1996; Warrick and Dial 1998) and behavioral differences correlate with the wing designs of various species (Tobalske, Peacock and Dial 1999).

We observed in our discussion of form, function, and character for feather origination that multi-functionality prevents only one uniquely correct character from being isolated for analysis. In the case of flight, the multiple structural units and sub-functions that come together in the production of flight activity reveal a methodological asymmetry in investigating innovations and novelties because the function is dependent on the existence of multiple structures. More abstractly, one form can yield multiple functions (one → many) whereas one function is dependent on many structural components (many → one). This asymmetry extends into the paleontological component of the analysis where structural features are more readily available. The inference from structure to function is not straightforward (Lauder 1995). A variety of phylogenetic, non-phylogenetic, and 'functionally' calibrated methods of inferring behavioral features related to flight origin have been catalogued (Arnold 2001). These include looking for correlated traits within clades (presence of one trait makes presence of another likely), analyzing organisms as machines (biomechanical, engineering considerations), and persistent traits (a feature is 'virtually' irreversible once obtained). When these methods are applied to the posterior directed hallux (first toe) of *Archaeopteryx*, one can infer that it probably grasped twigs and perched, lived in a lagoon environment, did not climb using its forelimbs, and spent substantial time on the ground, though arboreality cannot be ruled out (cf. Hopson 2001).

The asymmetry of one form exhibiting many functions and one function being the result of many forms does not preclude beginning an investigation with either a form or a function. The selected feature is complemented to produce one character (among many possible) for analyzing the origin of the particular form or function under scrutiny. Each case is procedurally conditioned by these asymmetries. This heightens the significance of using different characters as theoretical units of integration in understanding the origin of form and function. Often character choice is executed implicitly but only negatively, in order to discount particular explanations of form or function features under consideration. Rayner and Dyke have explicitly taken the wing as a character and analyzed its evolutionary trajectory as an aerodynamic thrust generator (i.e. as an airfoil), showing that, despite skeletal differences in the forelimb, the requisite shape was in place in the theropod lineage (Dyke and Rayner 2001; cf. Middleton and Gatesy 2000) and subsequently diversified with avian lineages (Rayner 2003).

3.3.6. How does the recognition of distinct levels of biological organization apply to the origin of this feature? Can we distinguish pertinent compositional and procedural hierarchies, either developmentally (spatially) or evolutionarily (temporally)?

Many of the skeletal modulations correlated with flight appear at high levels of organization: overall lightness, enlargement of braincase, vertebral column adjustments (e.g.

increased neck vertebrae; few caudals and pygostyle for long bony tail), shoulder girdle for flight stroke, and forelimb modification, such as restriction of range of motion and digit loss (Chatterjee 1997; Feduccia 1996; Paul 2002). A variety of compositional hierarchies exist for the main structural unit involved in the flight stroke, the wing. These different anatomical units (muscles, skeletal elements, and innervations) and their functions must be in place for the wing to be able to 'flap'. In addition to those features nested within the wing, consideration of the anchoring of the pectoral muscles in the coracoid and sternum is also necessary, as well as shoulder girdle shape. The significance of these compositional hierarchies was sketched above (Section 3.3.5) where we observed that focusing on characters draws attention to the fact that multiple form aspects or morphological parts underlie flight stroke activity. Any treatment of the origin of flight requires attention to a host of nested subparts that are prerequisites for the ability to accomplish powered flight. Additionally, the execution of the flight stroke involves procedural hierarchies in terms of the sequential firing of subunit muscles in a coordinated fashion. Whether these compositional hierarchies map onto procedural hierarchies during development is still unclear because ontogenetic studies of flight are sparse.

One relevant discussion of procedural hierarchies in evolutionary time has come from work on locomotion modules (Gatesy 1995, 2001, 2002; Gatesy and Dial 1996). Comparisons of locomotion-related anatomy for hypothetical, generalized archosaurians and hypothetical, ancestral birds reveal distinct differences in the degree of modularity in locomotion related units.[103] In archosaurian morphology, many anatomical sub-regions are inextricably intertwined during the performance of locomotion functions whereas birds have a much higher degree of modularity or independence of sub-regions (Farlow *et al.* 2000; Gatesy 2002; Gatesy and Dial

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[103] "Locomotor modules are anatomical subregions of the body that function as highly integrated units during locomotion [and] …are identified using data from electromyographic (EMG) analyses to assess each muscle's contribution to a locomotor behavior" (Gatesy 2002, 433-434).

1996). The avian locomotion system is highly partitioned in contrast to an almost uniformly integrated archosaurian locomotion system. This partitioning is tripartite with two main functional outputs: a pectoral (wing) module coordinates with a caudal (tail) module to create aerodynamic forces during flight whereas during bipedal movement a pelvic (hind limb) module is active. The origin of flight can therefore be partly understood as the modularization of the locomotion system in evolutionary time. In what precise sequence did this occur (procedural hierarchy in evolutionary time)?

Fossil forms permit a reconstruction of the hypothetical ancestral forms: *ARCHOSAUR* - quadrupedal, one locomotor module; *THEROPOD* - bipedal, one locomotion module with reduced functional requirements on forelimbs (Farlow *et al.* 2000); *PARAVES* - bipedal, one locomotion module with incipient divisions of pelvic and caudal function based on diminished caudalfemoral musculature size and importance, as well as a partial decoupling of hind limb and tail due to a more proximal and mobile tail that was both narrower and lighter; *AVES* – bipedal, distinguishable locomotor modules and flight ability, although less refined than observed in modern birds with slightly different hind limb function. Subsequent stabilization of the modules and independent evolution allowed for the locomotion systems observed in extant birds (Gatesy 1995, 2002; Gatesy and Dial 1996). Many other anatomical alterations correlate with these changes, such as reduction in tail length between *THEROPOD* and *PARAVES*.

A final relevant issue concerning procedural hierarchies in evolutionary time is the origin of appropriate neuromuscular control (Goslow, Wilson and Poore 2000). Paleontological studies described indicate that increased brain and optic capacity is associated with flying animals, indicative of increased neuromuscular needs, and originated prior to flight itself. Thus, procedural hierarchies in evolutionary time likely existed for nervous system and brain function transformations preceding the actual ability of flight, although some of these neuromuscular transformations may have occurred secondarily in coordination with the evolutionary diversification of flight. The details of these procedural hierarchies in ontogeny are very hazy even though their potential significance was recognized long ago (Maynard Smith 1952).

3.3.7. How does the issue of generality apply to the origin of the feature? How does the molecular paradox apply and what explanatory principles are available or relevant?

The generalized explanatory principles for the origin of avian flight are very different from those found in molecular developmental genetics. Foremost among these are biomechanical considerations derived from the application of physical principles to animal structure and function. For example, the activity of swimming becomes relevant for understanding flight because water and air can be treated as locomotive media with different fluid dynamics (Azuma 1992; Taylor and Nudds 2003). And just as there is more than one way to 'fly', there is also more than one way to 'swim': snaking, fanning, paddling, whipping, jetting, sweeping, beating, sailing, skating, and wave riding (Azuma 1992, ch. 5-7). The study of flight in insects and bats yields biomechanical principles that reciprocally inform studies of avian flight (Alexander 2002; Azuma 1992, 123-154; Birch and Dickinson 2001; Brodsky 1994; Clark 1977; Dudley 2000; Grodnitsky 1999; Norberg 1990a, 1990b; Wooton and Ellington 1991). For example, insects exhibit differing modes of flight such as flapping and hovering (Brodsky 1994; Dudley 2000; Grodnitsky 1999; Wooton and Ellington 1991). Key morphological features such as wings did not originate in conjunction with flight but were modifications of the respiratory apparatus, an ancestral leg segment, or thoracic/abdominal outgrowths (cf. Brodsky 1994;

Dudley 2000; Grodnitsky 1999; Wooton and Ellington 1991). Physical principles pertaining to aerodynamics can be generalized to flight origination in various taxa (Alexander 2002).

For the origin of avian flight, flight in pterosaurs and bats are most pertinent. Different types of vertebrate flight can be characterized and morphological features such as wing form, flight stroke, muscle and skeletal structure and arrangement, and body size can be assessed for 'dynamic similarity' across these widely disparate taxa (Azuma 1992; Neuweiler 2000; Norberg 1987, 1990a, 1990b; Padian 1985; Pirlot 1977; Rayner 1987, 1988, 2001; Smith 1977; Templin 1977). Comparisons of adaptive sequences in different phylogenetic contexts can reveal commonalities in the appearance of characters relevant to the origin of flight (Padian 1985, 1987; Rayner 1988). Studies of pterosaur wing morphology, function, and its aerodynamic properties provide a striking contrast to the origination of avian flight at a slightly earlier phylogenetic juncture (Alexander 1989, ch. 8; Padian 1983, 1985, 1991).[104] The neuroanatomy of some pterosaurs matches the cranial capacity increase observed in avian lineages, as well as having enlarged, semicircular canals indicative of equilibrium maintenance (Witmer *et al.* 2003).

Comparative studies of the prenatal and post-natal development of bat wings and hind limbs show novel patterns of skeletogenesis, myogenesis, growth rates, bone fusions, and shape changes (Adams 2000; Adams and Thibault 2000; Chen *et al.* 2005; Hermanson 2000; Schutt *et al.* 1994). The flight function emerges through a series of flight approximations: flopping behavior or falls without wing flapping (0-5 days post-natal); 'drop-evoked fluttering' (~10 days); flapping behavior (~17 days); and, 'actual' flight (~24 days) (Adams 2000). During this period there are dramatic alterations in functional capacities such as turning radius, wing loading, and aspect ratio due to rapid wing growth. Juvenile bats also exhibit differential resource

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[104] Juxtaposing fossils and fluid dynamics is also potentially illuminating, as in the evolution of 'underwater flight' in plesiosaur locomotion (Riess and Frey 1991).

utilization from adults prior to the onset of flapping flight (Adams 2000). Ecological niches correlate with flight mode, including migration (Norberg 1990a, ch. 7, 12; 1990b; Padian 1987).

Other applicable principles can be gleaned from unlikely places. A study on the origin of ‘flying’ frogs revealed a critical behavioral component in the evolution of this novel mode of locomotion (Emerson and Koehl 1990); apart from particular behavioral modifications, a structural change was detrimental *rather* than beneficial to performing the activity. Also, the critical performance parameter was not distance of horizontal travel but maneuverability. Gliding tree snakes provide another contrastive study as they achieve their flight mode without appendages largely through the performance of undulatory movement coupled with the maintenance of a concave ventral shape while in the air (Socha 2002). Profitable comparisons can even be made with invertebrates, as a study of neuromuscular organization in pteropod mollusk appendages and bird wings revealed common components for flapping locomotory capacities (Welsford *et al.* 1991).

Another domain of generality is physiology. The physiology of flight makes certain demands of energetic efficiency, metabolic rate, respiration, and circulation that can be applied to disparate taxa (Norberg 1990a, ch. 2; Ruben *et al.* 1997; Ward *et al.* 1999). Blood respiratory properties and heart rates are similar between bats and birds (Thomas 1987). The metabolic gaps sometimes cited between birds and mammals on the one hand and dinosaurs on the other are not prohibitive (Paul 2002, Appendix 4; but see Ruben and Jones 2000; Ruben *et al.* 1997).

In closing this section we can make two observations about the model organism issue regarding the origin of avian flight. First, there is much higher taxonomic sampling, both extant and extinct, for biomechanical and functional morphological studies of flight origination, including locomotion in theropods and post-natal growth/activity. Thus, the basis from which to generalize about the role of particular muscles or skeletal elements is fairly robust. But this increased taxonomic sampling does not necessarily confront the dilemma of having taxa relevant to the phylogenetic juncture where flight originated. Given that the goal is an explanation of the transformation from an ancestral genotype-phenotype mapping relation to a descendant mapping relation for a qualitatively different feature, increased taxonomic representation may not give the *particular* representative taxa needed to elucidate the causal mechanisms of the origin of variation at the particular phylogenetic juncture. This potential difficulty is exacerbated by the relative lack of ontogenetic studies of functional variation bearing on flight performance. And, although the molecular paradox is just as applicable to functional variation pertaining to the capacity of flight, the absence of molecular developmental genetic details means that its significance cannot be evaluated in our current state of knowledge.

3.3.8. What major research questions are associated with the origin of this feature? What kinds of solutions have been offered?

Researchers interested in the origin of avian flight recognize the issue of testability lurks amidst many of their questions (Witmer 2002).[105] But a sampling of pertinent research questions can be extracted from our foregoing discussion.

a) What developmental processes are involved in wing morphogenesis (including its components)? What developmental processes are involved in the performance of the activity of flight? Can we correlate any molecular genetic expression with the ontogeny of flight? Can we demonstrate 'forelimb' assisted incline running in non-avian animals?

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[105] "It is conceivable that the origin of flight-as a matter of scientific discourse-is out of reach. We may simply never have the appropriate data to adequately test any models" (Witmer 2002, 17).

b) Can denser taxonomic sampling allow us to more precisely reconstruct a hypothetical common ancestral flying apparatus for the theropod lineage that gave rise to birds?

c) Can theropods with arboreal skeletal adaptations be unambiguously identified? Can theropods prior to *Archaeopteryx* be isolated showing more primitive flight capabilities?

d) How many different form features are absolutely required for achieving different flight modes? What are different decompositions of characters relevant for understanding the qualitative departure from an ancestral character state?

e) What is the exact nature of a compositional hierarchy of the flying apparatus? Are there procedural hierarchies with respect to neuromuscular features that can be identified ontogenetically? How would we understand them phylogenetically? Can we discern procedural hierarchies of behavior related to achieving flight capacity in post-natal birds?

f) Did bat flight originate through a hovering stage? What is the best analogous model for bird flight origination, pterosaur or bat flight? Should we pay more attention to reptilian locomotive dynamics?

Answering some of these research questions may seem out of reach at the moment and yet new evidence, such as WAIR (Dial 2003), has recently emerged.

Despite the difficulty of adequately addressing these questions, putative solutions have been offered for the origin of avian flight. One is the cursorial theory (Padian 2001a; Padian and Chiappe 1998; Padian, Qiang and Shu-An 2001). The key issue is the generation of a flight stroke to generate the lift or thrust needed for powered flight (Padian 2001c). The transition can be understood as a functional switch from a predatory stroke to a flight stroke via multiple skeletal, neurological, and behavior alterations (cf. Gauthier and Padian 1985; Gishlick 2001):

elongated hands were protracted along the joint of the semilunate carpal (allowing protraction, retraction, and rotation); further elongation of arms and hands changed shoulder joint orientation; innervations altered for flight stroke function along with behavioral modifications; and, elaboration of feathers produced a competent airfoil. The primary objections leveled at cursorial models of flight origin concern the difficulty of working against gravity and the need for a rapid running speed to get off the ground (Feduccia 1996; Geist and Feduccia 2000; Norberg 1990a; Rayner 1988; Tarsitano *et al.* 2000; cf. Jones *et al.* 2000a). Despite these obstacles, ground-up modeling of flight origination can be made biomechanically feasible, especially when control over body maneuvering is factored in (Caple, Balda and Willis 1983).

Two types of studies have given cursorial theories a boost in recent years, blunting objections concerning the aerodynamic problems with ground-up hypotheses. The first was a study of *Archaeopteryx* that demonstrated how non-avian maniraptoriforms could generate thrust from flapping motion (Burgers and Chiappe 1999) and that thrust is more critical than lift to achieving flapping flight from the ground-up (Burgers and Padian 2001), assuming the possession of aerodynamically appropriate wings of sufficient strength (Rayner 1991, 2001). The second is studies of wing-assisted incline running in juvenile and adult birds (Bundle and Dial 2003; Dial 2000, 2003). The cursorial theory does not preclude a role for gliding in the origin of the flight stroke (cf. Norberg 1985; Rayner 1988, 1991).

Although it is not a logical prerequisite, most arboreal theories of flight origination explicitly eschew the phylogenetic context offered by contemporary phylogenetic systematics. For example, Feduccia gives the following stages on the assumption of a ‘thecodont’ ancestral form (Feduccia 1996, ch. 3; cf. Geist and Feduccia 2000).

i. Small, ancestral basal archosaur with quadrupedal terrestrial locomotion and mesotarsal joint (Early to Mid-Triassic)
ii. Arboreal life, small size, increase in brain and eye size, quadrupedal locomotion, elongate forearms, leaping between branches and trees, patagial membranes (Late Triassic)
iii. Parachuting stage, quadrupedal pre-proavis with featherlike scales or arm feather used in feather assisted jumping; beginning digital reduction (Late Triassic)
iv. Gliding proavis, early feathers, eventual release of arms, incipient bipedal perching, incremental growth of cerebellum and cerebral hemispheres (Early Jurassic)
v. Primitive powered flight (*Archaeopteryx*), incipient obligate bipedality, reversed hallux, perching ability, wing claws to aid balance, trunk-climbing ability, full body contour feathers, quasi-ectothermy, primitive powered flight (Mid- to Late Jurassic)
vi. Modern endothermic carinate birds, keeled sternum, triosseal canal, fully developed flight architecture, pygostyle (Early Cretaceous)

The transition from gliding flight to flapping flight has been aerodynamically modeled and is quite biomechanically feasible (Norberg 1985, 1990a; Rayner 1988). Most researchers agree that *Archaeopteryx* was capable of powered flight even if it was primitive (Burgers and Chiappe 1999; Chatterjee 1997; Chatterjee and Templin 2004; Paul 2002; Rayner 1988, 1991, 2001). Although this scenario is attentive to the functional morphological alterations involved in avian flight origins (cf. Geist and Feduccia 2000; Homberger and De Silva 2000, 2003; Tarsitano *et al.* 2000), it ignores a rigorous phylogenetic context, a substantial chunk of paleontological findings, and developmental information. Independent objections to arboreality also exist, such as the lack of trees in the paleoecology of *Archaeopteryx*. Other arboreal theories are more attentive to systematics but still ignore developmental considerations (Chatterjee 1997; Chatterjee and Templin 2004; cf. Paul 2002). Overall they share a core set of postulated stages: arboreal leaping, parachuting, gliding, and then flapping flight.

3.4. Conclusions and Remarks on Organizing Scientific Research

One way to understand the strategy of this chapter is in terms of *organizing* the concrete research questions that scientists actually utilize *with* the abstract notion of a problem agenda. Abstract philosophical constructs need to be recognizable by scientists even if they are not operationally deployed (Griesemer 1984). By working through the details of the origin of feathers and flight, it should now be clear how the problem agenda of innovation and novelty is manifested in research surrounding dinosaur, reptile, and avian biology. It should also be clear how problem agendas are composed of multiple questions of different kinds, reiterating the value of the move *from* problems *to* problem agendas articulated in Chapter 2. Even if some of these research questions are answered, it does not imply a complete solution to the mechanistic origin of variation at particular phylogenetic junctures for avian feathers or flight; the addition, deletion, or transformation of these questions does not necessarily change the subject matter of inquiry. Additionally, the decoupling of methodology from problem agendas is more perspicacious. Problem agendas require multiple methodologies from different biological disciplines but methodologies can come and go in the midst of problem agenda stability.

One outcome of the preceding discussion is a more transparent account of where different disciplines need to make contributions in order to address the criteria of explanatory adequacy (cf. Maderson and Homberger 2000). But the interdisciplinarity is revealed to be different for the two features under consideration, let alone that the question of bird origins falls under a different problem agenda. Thus, although Prum's three questions adumbrated at the outset of the chapter may be perceived as 'inextricably linked' (Maderson and Homberger 2000), they are conceptually separable upon further analysis. The origin of feathers demands contributions from systematics that focus on taxa with and without the relevant feature; paleontological and morphological analysis relevant to that feature;[106] developmental studies that concern feather morphology and archosaurian integument; functional morphological studies that attend to different functions that feathers could have for biological characters in organisms; attention to morphogenetic procedural hierarchies; and, input from developmental systems bearing on feathers such as hair follicle formation. In contrast, for the origin of flight, systematics makes a slightly different contribution to explaining avian flight because the ancestral condition in focus is different; paleontological analyses concentrate on different morphological features; the few developmental studies attend to later ontogenetic events apart from developmental genetic patterning; functional morphological studies concentrate on physical principles of a heavier-than-air object propelling itself continuously off the ground along with the requisite skeletal and muscular dynamics; procedural hierarchies in time with respect to locomotion must be attended to; and, a host of other 'flying' organisms are relevant in terms of biomechanical principles and functionally analogous performance during flight. In both cases, particular disciplines make distinct and necessary but not sufficient contributions to the overall explanation.

One set of disparities worth dwelling on further is found in the degree of generality dimension. Taxa bearing evolutionary innovations and novelties *from* which or *to* which studies of feather origination and flight origination might generalize are drastically different. But not only is there a difference in taxa, there is a difference in the kinds of data and analyses from which to generalize. Studies of feather development must face the molecular paradox when attempting to offer explanations of the origination of complex feather morphology. Although the applicability of the molecular paradox for flight is somewhat unclear due to a lack of ontogenetic

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[106] I have not been as explicit in this chapter about flagging the contribution from morphological investigation in the origin of feathers but much of the paleontological research depends on it and all of the work on the histology and morphology of feathers in the integument are morphological studies (cf. Bereiter-Hahn, Matoltsy and Richards 1986; Homberger and De Silva 2000, 2003; Lucas and Stettenheim 1972a, 1972b).

data, many domains of generalization concern biomechanical principles derived from functional analyses under analogous conditions. Sufficient attention to the disparities regarding generality indicates why evolutionary innovations and novelties that appear to be related actually need their investigation prosecuted much differently.

Several advantages are gained from formulating these issues with the problem agenda tool. These will be revisited in later chapters and are indicators of significant features surrounding explanations of evolutionary innovation and novelty. First, disciplinary contributions cannot occur in parallel. The contribution of some disciplines is methodologically prior to others in executing a full analysis. Most obviously this issue arises for the systematics contribution, which sets a phylogenetic context necessary for investigating the mechanistic origins of variation at a particular phylogenetic juncture (Lauder 1990; Lauder *et al.* 1995; Weishampel 1995).[107] This is not to say that biologists from different disciplines cannot execute research simultaneously but rather that contributions to an integrated explanation of a particular innovation or novelty have methodological ordinality; particular disciplinary contributions are conditioned by other specific contributions. Second, the asymmetry of investigating form versus function brings different issues to understanding the evolutionary origination of a feature. Because form features exhibit multi-functionality and multiple structural features realize most functions, the significance of the role of character (form/function complex) analysis is paramount. An emphasis on the relation between form and function in biological characters, especially at higher levels of organization, highlights the need for morphological investigations in addition to molecular developmental genetic ones, which also arose in the context of the molecular paradox.

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[107] To be strictly faithful to our aim of decoupling methodology from problem agendas, cladistics cannot be the *necessary* methodology for reconstructing phylogeny, though it is currently the preferred method for doing so.

A final aspect of making the criteria of explanatory adequacy more explicit is the recognition of the difficulty of offering a *complete* solution. In order to have ongoing interdisciplinary work of the sort articulated, a symposium at an annual meeting (Maderson and Homberger 2000) or special issue of a journal (Chuong and Homberger 2003) cannot be considered sufficient. The dimension of generality also brings into focus how certain aspects of avian flight ontogeny, especially post-natal juvenile development, require further study. Investigators of bat flight evolution and avian locomotion have explicitly recognized the need for interdisciplinarity, including the study of juvenile ontogeny, morphology, and function (Adams and Pedersen 2000; Gatesy 2002).[108] How the abstract account of a problem agenda, its individuation, and its characterization connects with concrete examples of specific phenomena that fall within the explanatory range of that problem agenda, such as feathers and flight, should now be far less opaque.

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[108] "Advances in our understanding the evolutionary history of the avian locomotor system will require a synthesis of hypotheses from specialists in different areas" (Gatesy 2002, 445).

4. HISTORICAL INVESTIGATIONS OF INNOVATION AND NOVELTY

4.1. Introduction

This chapter contains historical investigation of the concepts of EVOLUTIONARY INNOVATION and NOVELTY in explanations of biological phenomena. By necessity, it cannot be exhaustive of concept use over the past seventy years (the period of supposed ‘negligence’ claimed by Evo-devo proponents) but the requisite data for analysis can be gleaned through sketches of broadly relevant themes and close attention to a few particular researchers. Section 4.3 identifies these large-scale patterns and subsequent sections treat individual researchers of the middle 20th century from particular biological disciplines that focused on innovation and novelty in biological explanations: N.J. Berrill (comparative embryology), D. Dwight Davis (morphology), and William K. Gregory (paleontology). The decision to look more closely at these three individuals is motivated by the observation that contemporary developmental genetic approaches to explaining innovation and novelty have skewed the investigation of historically relevant material for Evo-devo. Section 4.2 probes the intersection between a history of innovation and novelty and histories relevant for Evo-devo, where a distinction is drawn between the problems of researchers and the tools used to investigate them in order to provide a historiographic principle of choice.

4.2. A Historiographic Principle of Choice: Evo-devo History from the History of Innovation and Novelty

4.2.1. Genetics and Embryology Exclusion Histories and Problems versus Tools

Exploring history pertinent to Evo-devo is an exciting prospect given its current status as a cutting-edge field of research. At the same time, there are pitfalls to writing histories of this fledgling 'discipline'. The first and obvious question is where to begin searching for materials and sources. Historians and philosophers have directed attention to many individuals, disciplines, and institutional contexts relevant from the history of evolutionary studies and investigations of ontogeny (e.g. Allen 1986; Bowler 1996; Burian, Gayon and Zallen 1991; Gilbert 1991b; Maienschein 1991). But are these the only appropriate historical antecedents of the emerging discipline of Evo-devo? Since histories of evolutionary ideas and developmental studies encompass a wide range of persona, place, and professional affiliation, a cohesive narrative may be elusive.

Another strategy is to take a cue could be taken from how the contemporary 'endpoint' of the historical study is being conceptualized. Hall has drawn a multifaceted portrait of the current composition of Evo-devo (cf. Section 1.1 on disciplinary syntheses).

> For evolutionary developmental biology (EDB or 'evo-devo') is not merely a fusion of the fields of developmental and evolutionary biology, the grafting of a developmental perspective onto evolutionary biology, or the incorporation of an evolutionary perspective into developmental biology. EDB strives to forge a unification of genomic, developmental, organismal, population, and natural selection approaches to evolutionary change. It draws from development, evolution, paleaeontology, molecular and systematic biology, but has its own set of questions, approaches and methods. (Hall 1999a, xv)

Following our caution about an overarching and cohesive narrative, Hall's portrayal (and others) suggests that historical material from molecular biology and systematics, as well as paleontology, may be pertinent for understanding how we arrived at the present situation. Yet disagreement about the composition of Evo-devo (what it is, what disciplines it should be composed of, and what its key questions are) might suggest that the history of these other areas is irrelevant. The depths of relevant historical aspects of Evo-devo are being mined on several fronts that should keep the possible heterogeneity of past inputs to the present in view (e.g. Gilbert 2003a; Hall 2000, 2003b, 2005; Jenner 2004; Laubichler 2003, 2004; Laubichler and Wagner 2003; Levit, Hoßfeld and Olsson 2004; Maienschein and Laubichler 2004; Wagner and Laubichler 2004). Although Hall's presentation is not idiosyncratic (cf. Raff 1996, 2000; Wagner, Chiu and Laubichler 2000), a principle of choice for delineating appropriate sources for exploring history pertaining to Evo-devo needs explicit articulation.[109]

A principle of choice is also necessary because an implicit historiographic premise has been present in recent historical research relevant for Evo-devo. In the attempt to comprehend the separation between evolution and development much attention has been paid to the split between genetics and embryology in the early part of the 20th century with the codification of this fissure in the exclusion of embryology from the Modern Synthesis. This encourages a characterization of Evo-devo in terms of developmental genetics as a bridge between genetic accounts of evolution and a molecularized embryology (developmental biology). Both biologists and philosophers have overemphasized developmental genetics in their retelling of histories related to Evo-devo, mistaking the current prevalence of molecular genetic embryology for the variegated research programmes that continually kept the relationship between evolution and development in view (cf. Love 2003a; Love and Raff 2003; Raff and Love 2004).

It is an oft-repeated historical claim that embryology was excluded from the Modern Synthesis (Hamburger 1980), or at least that embryologists did not want to participate (Mayr

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[109] Identifying historical sources relevant for Evo-devo is not the same as documenting the influence of these sources (a more difficult task). Since the primary goal of our study concerns conceptual use regarding innovation and novelty, I will not fully establish the influence of the relevant historical sources. In several cases I indicate evidence that points toward direct influence but other evidence bearing on this is not included.

1993). This exclusion is frequently perceived as a source for the foundational problems attending contemporary evolutionary theory that require the synthesis called Evo-devo.[110] Many historians have documented the historical trajectories of genetics and embryology, their split, and various relations, or lack thereof (Allen 1985, 1986; Gilbert 1978; Maienschein 1987; Sapp 1987). Much of this story transpires in the first three decades of the 20th century, as genetics became an autonomous discipline. Assuming genetics and embryology were separate by about 1935, the tight connection between population genetics and evolutionary theory in the Modern Synthesis helps explain the exclusion of embryology. Although some key participants had resources for bringing embryology into the discussion, by and large this simply did not occur.[111]

For example, Julian Huxley's training in and passion for experimental embryology (Huxley and de Beer 1963 [1934]) and his work on relative growth (Huxley 1993 [1932]) would have made him a likely candidate to discuss the importance of development for evolution in his contribution to the synthesis (Huxley 1942). Arguably, ontogeny was preeminent among Huxley's diverse biological interests, especially in his laboratory work, and he seemingly remained aware of the evolutionary consequences of these studies (Witkowski 1992). Despite this potential, when Huxley treats ontogeny under "three aspects of biological fact" ("the mechanistic-physiological aspect: how is the organ constructed, how does the process take place?") in *Evolution, the Modern Synthesis* (1942), he equated this developmental component with the *transmission* of hereditary factors when mapping the three aspects onto their evolutionary counterparts (Huxley 1942, 40-1). His only discussions of ontogeny focus on rate genes (525-543), which is curious because this perspective is not adopted in his text with de Beer

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[110] Other historical developments in biology, such as phylogenetic systematics, could not have been part of the Modern Synthesis in the 1940s since they emerged at a later date.

[111] The Modern Synthesis was a heterogeneous phenomenon and the principle aspect in view here concerns mechanisms of evolutionary change in terms of genetics (population or otherwise) with or without a developmental component. For example, I am not addressing perspectives on systematics in the Modern Synthesis.

from eight years earlier. There the 'gradient field' is a key organizing concept and levels of organization 'above' the cell are prioritized over genetic phenomena (Churchill 1992, 116-126; 1993; Witkowski 1992). All mention of allometry having "an immediate bearing upon certain evolutionary problems" or any "further evolutionary implication of these facts" has disappeared (Huxley 1993 [1932]).[112]

The genetics and embryology histories of separation and subsequent exclusion are not necessarily incorrect in their details but a concern arises over how they have been put to use.[113] If evolution is understood primarily in terms of genetics (which is not unusual given the welding of evolutionary theory to population genetics in the Modern Synthesis and later emergence of molecular genetics), then a synthesis of evolutionary and developmental biology calls for a bridge between 'genetics' and 'embryology'. Recent results from comparative studies in developmental genetics appear to provide a link between genetically based accounts of evolutionary mechanisms and molecularly characterized developmental processes (Carroll 1995; Carroll, Grenier and Weatherbee 2001; Marshall, Orr and Patel 1999). The historiographic premise of the 'crux' lying with the separation of genetics and embryology is serving as a normative template, in conjunction with the success of molecular developmental genetic investigations, for constructing research programmes such as Evo-devo.

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[112] A partial explanation can be derived from Churchill's analysis of *The Elements of Experimental Embryology* (Churchill 1992). In a table used to track Huxley's various publication topics over time (112-113), Churchill shows that Huxley's interest in things embryological largely ends in 1934-5 and his publications on the topic of evolution consequently begin. Huxley did not truly synthesize his work on development with his evolutionary thinking, which appears very similar to T.H. Morgan's difficulty of bringing genetics and embryology into textual proximity without genuinely integrating them (Morgan 1934). The case of Goldschmidt is interconnected with Huxley because of rate genes and sexual determination phenomena, but also significantly differs. It has been discussed extensively elsewhere (Churchill 1993; Dietrich 1995; Gould 2002, 451-466). I ignore it here because any potential contribution to the Modern Synthesis was screened off by active rejection, conceptually and sociologically, of Goldschmidt's ideas and persona. Huxley is clearly in the opposite position, and for that reason, interesting to consider.

[113] If the Modern Synthesis is construed broadly to include research that was not widely known or incorporated (e.g. work in non-Anglophone journals), then evaluating the 'exclusion' of research emphases becomes more difficult (Reif, Junker and Hoßfeld 2000). This is a reminder that national differences may play a role in the conceptualization of disciplinary syntheses (cf. Mayr and Provine 1980, 229-384).

The historiographic premise that focuses attention only on the fissure between genetics and embryology with an aim to prescriptively direct research can be observed in several places. In an article on the future of Evo-devo, Peter Holland claims: "Three main factors have contributed to the emergence and phenomenal growth of [Evo-devo]. Ironically, all three depend on genetics – the discipline that split evolution and development apart 60 years earlier" (Holland 1999, C41).[114] In sketching the possibilities for 'significant advance' he highlights the importance of attending to the limits of conservation, the role of regulatory mutations for understanding the link between genotype and phenotype, and gene duplication events. The 'radical alteration of genetic systems', such as genome duplication, is marked as critical for dissecting innovations in the history of life (C44). In closing, he encourages the 'embrace of genomics' as a rich future opportunity for Evo-devo.

In his well-respected textbook on developmental biology, Scott Gilbert concludes his recounting of the dramatic results from recent developmental genetics as follows:

> In the 1990s, the techniques of molecular biology enabled biologists to discover (1) homologous regulatory genes such as *Pax6* that control the development of the same organs thoroughout [*sic*] the animal kingdom, (2) homologous developmental pathways whose functions can change between organisms or between cells of the same organism, and (3) the changing patterns of the homeotic gene expression that allow different parts of the body to have different structures and functions. Such discoveries have converged to form a developmental evolutionary synthesis that incorporates the population genetic approach but which expands evolutionary theory to explain macroevolutionary phenomena as well. …We are at a remarkable point in our understanding of nature, for a synthesis of developmental genetics with evolutionary biology may transform our appreciation of the mechanisms underlying evolutionary change and animal diversity (Gilbert 1997, 914).

Gilbert implicitly equates the population genetic approach with evolution and sees developmental genetics as the key component missing from the synthesis.

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[114] The three genetic factors are: (1) conserved developmental genes that play similar functional roles in ontogeny across widely divergent taxa, (2) molecular phylogenetics, and (3) technical advances in molecular biology such as PCR and *in situ* hybridization, allowing for sophisticated analysis and manipulation of genetic material.

> Developmental biology complements the population genetics approach to evolutionary biology…. To explain evolution, both the population genetics and the developmental genetics accounts are required. …The merging of the population genetics model of evolution with the developmental genetics model of evolution is creating a new evolutionary synthesis that can account for macroevolutionary as well as microevolutionary phenomena (Gilbert 2000a, 705-6).[115]

In *Keywords and Concepts in Evolutionary Developmental Biology* (Hall and Olsson 2003), Gilbert and coauthor Burian write back-to-back articles, one entitled "Development, Evolution, and Evolutionary Developmental Biology" and the other "Developmental Genetics". In the former they suggest that "[Evo-devo] seeks to amplify and extend the modern synthesis of evolutionary biology and genetics to include developmental genetics as well as population genetics" (Gilbert and Burian 2003, 68).

Another example of this viewpoint is seen in Wallace Arthur's writings on Evo-devo.

> The goal of evolutionary developmental biologists is to explain the causality of this pattern, through consideration of how natural selection (the domain of population genetics) interacts with the genetic architecture of development (the domain of developmental biology). …the picture that [the developmental geneticists] ultimately produce (of which our current view is fragmentary but enticing) is likely to be the most important remaining input into evolutionary theory (Arthur 1997, 32, 43).

> Over the last twenty years, there has been rapid growth of a new approach to understanding the evolution of organismic form. … [Evo-devo] is focused on the developmental genetic machinery that lies behind embryological phenotypes, which were all that could be studied in the past (Arthur 2002, 757).

Again, population genetics is the core of evolutionary studies and developmental genetics is the 'missing link'. This perspective is enhanced through a diagram of the 'circle' of evolutionary theory (Figure 1). The major part of the 'missing' developmental component is developmental

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[115] Gilbert's textbook remarks both summarize a widely held viewpoint and represent aspects of his own nuanced account. E.g., "Classical evolutionary theory considered evolution a subset of population genetics and explained natural selection in terms of changes in gene frequencies. …The present synthesis of evolutionary biology and developmental genetics provides a different, and complementary, view of the roles of genes in evolution" (Gilbert and Bolker 2001, 452; cf. Gilbert 2003b).

genetics. Paleontology, comparative anatomy, and comparative embryology only contribute to our understanding of evolutionary pattern rather than process (cf. Arthur 2004b).

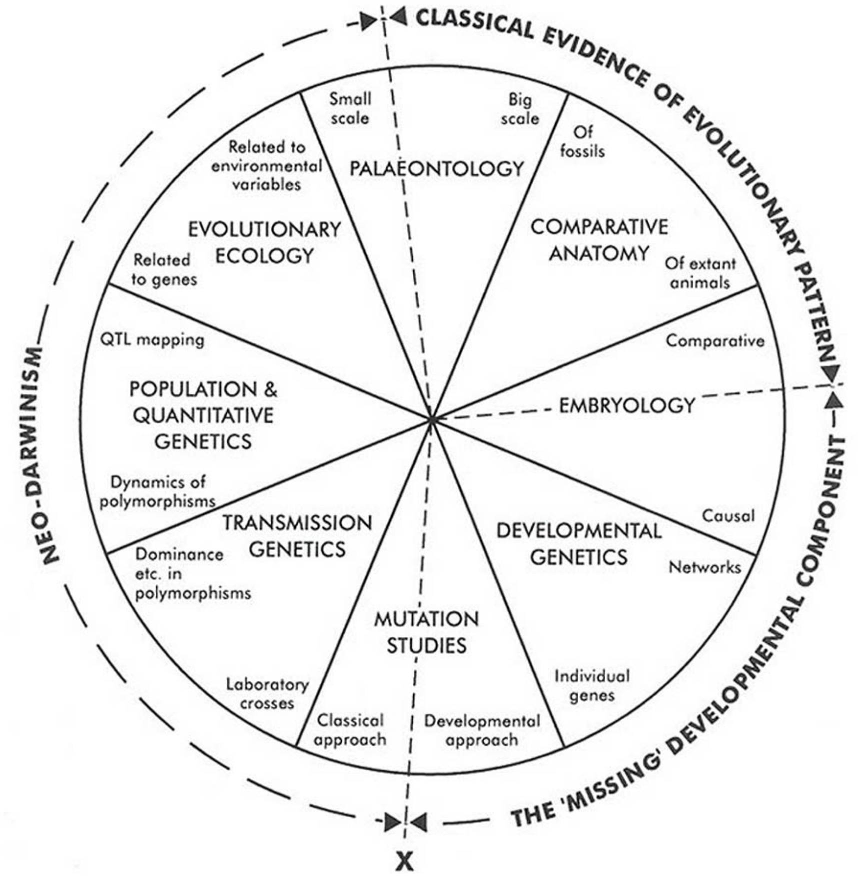

Figure 1: Disciplinary 'Circle' of Evolutionary Theory

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Although these examples are derived from the writings of individuals who perceive themselves as working within Evo-devo,[116] this perspective is identifiable elsewhere. In a chapter on 'Development and evolution' from a paleobiological textbook, the heading

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[116] It is also present in an overview of key concepts and terminology in Evo-devo: "With the advent of the Modern Synthesis, neither cell lineage studies nor the relationship between ontogeny and phylogeny were regarded as modern topics in evolutionary biology. However, that all changed with the discovery of regulative genes" (Hall and Olsson 2003, 245).

‘Integration of developmental biology with the evolutionary synthesis’ only discusses the importance of *Hox* clusters (Carroll 1997, 258-262). Under the heading ‘Evolutionary developmental biology’ in a book on zoological systematics, the following is found: “A completely new approach to animal evolution has grown out of studies of the genetic background of mutations in *Drosophila*. These studies have shown how various genes control the development of axes and domains” (Nielsen 2001, 515). This perspective is also utilized in a major undergraduate textbook where the section on Evo-devo is given the subtitle, ‘Genes that control development play a major role in evolution’ (Campbell and Reece 2002, 478-480). Additionally, some philosophers have framed the issue in terms of reuniting embryology and genetics. Amundson’s main investigative question and concluding remarks from a recent paper imply the ‘bridge’ of developmental genetics.[117] In the introduction to a symposium on Evo-devo, Richard Burian sees the control of eye formation by a conserved genetic module as a prominent example of how Evo-devo is unfolding.

> The extraordinarily rich details regarding integrated units that function in development, with controls that are preserved through even hundreds of millions of years, provide us with the materials to bring developmental, evolutionary, and genetic techniques to bear on old, but transformed, problems. This triangulation, I believe, will be the key to the success or failure of Evo-Devo (Burian 2000, 714).

Burian’s triangulation observation follows a variety of historical comments that imply that the key disciplinary split was between embryology and genetics in the early 20th century (713), a claim made even more explicit in an earlier article (Burian 1997).

Most of these portrayals of Evo-devo as a disciplinary synthesis concentrate on only two disciplines, population genetics and developmental genetics, in contrast to the multidisciplinary

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[117] “*Was the success of the Evolutionary Synthesis a factor in the increase of interest among embryologists in the study of developmental genetics*? … Unification of developmental with evolutionary biology has not yet been achieved despite the advances in developmental genetics” (Amundson 2000, 315, 327).

synthesis described by Hall.[118] A synthesis between population and developmental genetics fits snugly within the confines of the genetics and embryology exclusion histories, but does the synthesis of Evo-devo include non-genetic disciplines such as morphology or paleobiology? Even granting a pivotal role for developmental genetics in the renaissance of research on evolution and development, there are indicators that other disciplines played just as critical of a role, potentially even as a prerequisite for the advent of developmental genetics. Despite claims to the contrary (Arthur 2002, 2004b; Wilkins 2002), the recent revival of interest in the intersection between evolution and development can be traced back prior to the developmental genetic discoveries of the early 1980s.[119] Morphological and paleontological researchers jointly stimulated conversations about how results in developmental biology might impinge on the received view of evolutionary theory ('neo-Darwinism'). Most famous is the Dahlem conference of 1981 (Bonner 1982), as well as work on heterochrony (Alberch *et al.* 1979; Gould 1977) and systems-analytical approaches (Riedl 1977, 1978; cf. Wagner and Laubichler 2004). Although there was an early book recognizing the importance of developmental genetics for evolutionary change (Raff and Kaufman 1983), other discussions were quite heterogeneous (Goodwin, Holder and Wylie 1983). It is critical to stress that *relevant* history may not be equivalent to the history of why particular people are currently interested in a topic. Developmental genetic investigations of regulatory genes played a powerful causal role in

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[118] Other Evo-devo biologists perceive developmental genetics as the critical factor in awakening an interest in reuniting evolutionary and developmental biology, while acknowledging a broader range of disciplinary contributions (Carroll, Grenier and Weatherbee 2001; Raff 2000, 75).

[119] The referent of 'developmental genetics' in the above discussions is developmental genetics using recombinant DNA methodology (Fraser and Harland 2000). Developmental genetics is also an appropriate term for earlier research (such as Goldschmidt and Ephrussi) but this is not in view here. That this is the case can be observed in an introductory text on developmental genetics of 1971, prior to the advent of recombinant DNA technology (Markert and Ursprung 1971). Claims that development is best understood as the result of differential gene function are primarily programmatic via description of biochemical aspects of ontogeny and correlations with known transmission genetics (cf. Britten and Davidson 1971). (Perhaps 'molecular developmental genetics' is a better term, but it also contains ambiguities.)

drawing researchers back into the issues surrounding a juxtaposition of evolution and development, but this nexus of research predates molecular developmental genetics.[120]

Consonant with what has already been mentioned, the problem with these exclusion histories lies in taking the exclusion of embryology and rise of developmental genetics as the *whole* story for understanding the need to rejoin evolution and development in the present. The use of this history as the *primary* narrative for guiding the present construction of Evo-devo is a distortion, implying that the key rapprochement lies with developmental genetics, while forgetting others 'excluded' from the Modern Synthesis who might be critical to normatively directing and formulating the new synthesis of Evo-devo in the present.[121] Another way of highlighting the difficulties with this historiographic premise is to ask a straightforward historical question: what about *non-genetic* approaches to embryology?

Many of the contemporary *tools* for exploring the evolution of development have arisen by descent through the lineage of an experimental approach to embryology, most notably those from developmental genetics: molecular genetic manipulation, laser ablation, tissue recombination, bead implantation, *in vivo* electroporation, and various gene expression observation methods such as *in situ* hybridization and immunolocalization (Carroll, Grenier and Weatherbee 2001, ch. 2; Duffy 2002; Fraser and Harland 2000; Rapley and Walker 1998; Weaver and Hogan 2001). It is because of the predominance of these primarily genetic

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[120] Early expectations produced by the discovery of homeobox containing genes were often purely developmental, rather than immediately thought to bear on problems of evolutionary mechanisms. "Needless to say, this discovery has created much excitement, particularly because it is tempting to expect a similar set of conserved functions for homeo-box-associated genes in vertebrate organisms. If so, the highly conserved homeo-box sequence should then provide the molecular tag needed for identifying these genes in higher organisms" (Magnusson 1986, 461).

[121] My concern is whether the recent empirical success of developmental genetics is thought to be the core of Evo-devo because of a particular historiography, not whether the results of developmental genetics are significant. A side effect of the genetics and embryology exclusion historiography is a disproportionate focus on individuals such as Boris Ephrussi (Amundson 2000; Burian, Gayon and Zallen 1991), Richard Goldschmidt (Dietrich 1995; Gould 2002, 451-466), and C.H. Waddington (Amundson 2000; Gilbert 1991a, 2000b; Hall 1992), who can be seen as early participants in the bridge area of developmental genetics. In comparison, I.I. Schmalhausen has received less attention (but see Allen 1991; Gilbert 1994; cf. Levit, Hoßfeld and Olsson 2004).

techniques in contemporary developmental biology that this stream is seen as so crucial to the emergence of Evo-devo and leads to conceptualizing a reunion in terms of genetics (i.e. population genetics) and embryology (i.e. molecular developmental genetics) (Figure 2).

But if we shift our attention away from the tools of investigation to the agenda of problems within contemporary Evo-devo, experimental embryology is not the appropriate intellectual ancestor for most of the 20th century. Although overshadowed by the empirical success of experimental embryology and its descendent disciplines, many key issues such as phylogenetic relationships, the origin of evolutionary innovations, and significance of developmental constraints are the problems of comparative evolutionary embryology. These core agenda items are very much in the tradition of Kowalevsky, Haeckel, Gegenbaur, Balfour, and others that continued long after developmental mechanics constituted a thriving and distinct research program. Gavin de Beer, the most visible and influential theoretician in this tradition during the mid-20th century, has received some attention (Hall 2000; Brigandt forthcoming). His work primarily emphasized heterochrony, but probably more important was his ability to synthesize empirical studies to make general theoretical points (de Beer 1951; 1958, 1st edition = 1930). Most of the problems for contemporary Evo-devo researchers are lodged within the comparative evolutionary embryology tradition, where non-genetic tactics were standard (Gerson 2005; Love and Raff 2003; Raff and Love 2004; see Figure 3).

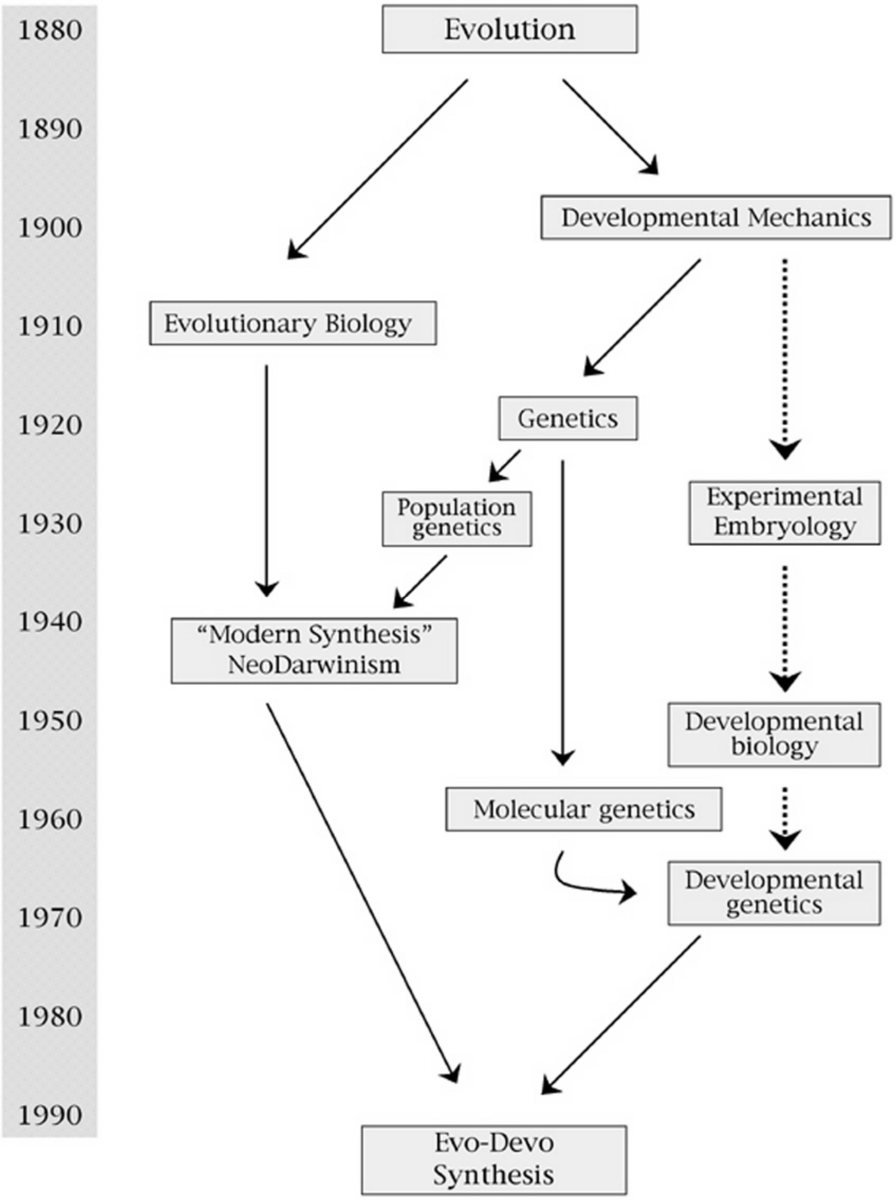

Figure 2: Genetics and Embryology Exclusion Histories Representation of the Embryological Contribution to Evo-devo

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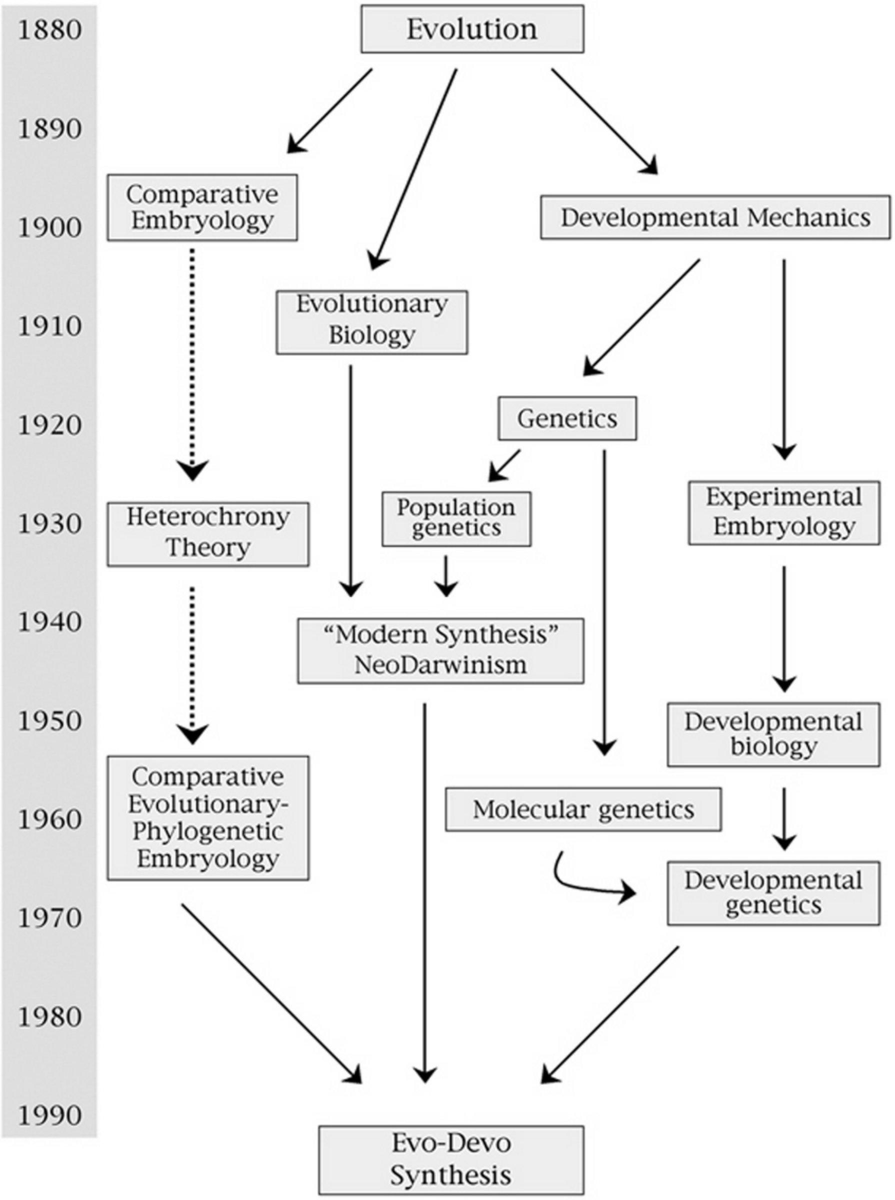

Figure 3: Problems versus Tools Representation of the Embryological Contributions to Evo-devo

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If we keep the *problems* vs. *tools* distinction in mind then we are driven to distinguish different kinds of embryology excluded from the Modern Synthesis and identify other disciplines that shared a common interest in these research questions.[122]

4.2.2. Problem Agendas and Historiographic Principles of Choice

Identifying the significance of the problems that exercise researchers interested in the intersection of evolution and development leads us to a working historiographic principle of choice in terms of scientific *problem agendas*, in particular the problem agenda of innovation and novelty as defined and delineated in Chapter 2. Succinctly, a history concerning aspects of a problem agenda relevant to a particular area of research today will also be a relevant (though not exhaustive) history for that research area. Evolutionary innovation and novelty have been persistently foregrounded by proponents of Evo-devo and this conceptual emphasis is connected with an explicit challenge to the sufficiency of neo-Darwinian evolutionary theory (see Chapter 1). This means that a historical study of the problem agenda of innovation and novelty is also a principled historical study of a core problem relevant to contemporary Evo-devo.

Problem agendas are often highly stable, emphasizing continuities rather than ruptures in contradistinction to many contemporary historical investigations of science (see Chapter 2). An interesting corollary to the longevity of the problem agenda of innovation and novelty is the stability of the scientific objects involved, i.e. the suite of phenomena described as evolutionary innovations or novelties. For example, 'the tetrapod limb' has been a stable entity for investigation for a long time (cf. Wagner and Chiu 2001; Westoll 1943b). The same phenomenon argued about 100 years ago remains a topic of investigation and was continually

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[122] It is important to observe that authors writing prior to the explosion of molecular developmental genetic research recognized this distinction (Grant 1985, ch. 33).

discussed throughout the 20th century. Other examples include the origin of feathers or characteristic features of vertebrates. In historiographic terminology, evolutionary innovations and novelties have been persistently *salient* (capturing scientific interest and having solidity as phenomena), *emerged* quite early in evolutionary research, have been periodically *productive* (in generating research programs that produce data and explanations, among other things), and have been continually *embedded* in networks of scientific practice, especially in morphological and paleontological research (Daston 2000).

One consideration in using problem agendas as historiographic principles of choice is the difficulty of anachronism. How can we be sure of semantic continuity between problem agendas as discussed in the present and problem agendas as articulated in the past? A problem agenda may have been captured with different terminology at earlier junctures. In fact, the problem agenda of innovation and novelty has often gone under the title of 'the origin of higher categories/taxa' or 'major transformations' (e.g. Bock 1965; Devillers 1965; Orton 1955; Schaeffer 1965; Simpson 1961). But a translation can be effected because the origin of new higher categories or major transformations in evolutionary history for earlier biologists was a problem of how particular, defining characters originated, which clearly falls within the problem agenda of innovation and novelty today.[123] Part of this translation requires attention to other developments in biological research. The phylogenetic agenda (problem agenda of classification) was interwoven with the problem agenda of innovation and novelty and the separation of these two is a relatively recent development (see below).

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[123] Recall from chapter 2 that we do not need to assume that researchers during this earlier period had theoretical constraints to distinguish the classification project from the study of innovations and novelties. We use theoretical resources from the present to identify relevant types of research from the past.

4.3. Patterns and Themes in the History of Innovation and Novelty (1930-1980)

4.3.1. Survey of Conceptual Use

A natural place to begin assessing historical themes in conceptual use for EVOLUTIONARY INNOVATION and NOVELTY from the early advent of the Modern Synthesis (~1935-40) to the 1980s is a seminal article by Ernst Mayr delivered at a Darwin centennial celebration in 1959 (Mayr 1960).

> 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" (349, my emphasis).

Mayr's main goal was to show how evolutionary novelties could be handled within the context of the synthetic theory of evolution without recourse to saltationism or macromutationism, both deeply connected with typological thinking in his estimation. Although his discussion broadly addresses the emergence of qualitatively new 'characters', he adopts a working definition of novelty that is functional in orientation in contrast to a structural definition more natural to the domain of traditional comparative anatomy: "Tentatively, one might restrict the designation 'evolutionary novelty' to any newly acquired structure or property which permits the assumption of a new function" (351).[124] Mayr ultimately reduces the project of explaining the emergence of evolutionary novelties to population genetics in sync with the Modern Synthesis theoretical framework: "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" (357). He also held that it was preferable to keep the origin of higher taxonomic categories distinct from the origin of novel

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[124] One of Mayr's motivations was to include metabolic pathways and animal behavior in discussions of evolutionary novelties, which did not seem to be 'structures' in the traditional sense of comparative anatomy. The language of chapter 2 captures these differences through the form (novelty) / function (innovation) distinction.

characters, which was necessary given that many researchers ran together the origin of novelties and the origin of higher taxonomic categories.

A quick glance at the citations available to Mayr on the subject of evolutionary innovation and novelties reinforces that the traditional 'homes' for discussions of innovation and novelty are comparative evolutionary embryology, morphology and paleontology (Love 2003a; Love and Raff 2003; Raff and Love 2004). There the key questions had little to do with explaining 'how a sufficient number of small gene mutations can be accumulated until the new structure has become sufficiently large to have selective value'. That morphological and paleontological researchers have been interested in this problem agenda (in addition to comparative embryology), and thereby attentive to the relationship between evolution and development, may appear trivially true. One can easily find paleontologists in the period from 1875-1910 utilizing the biogenetic law and biased variation due to ontogenetic trajectories in order to buttress theories of orthogenesis (Bowler 1996, 99-103; Gould 1977, 85-96; 2002, 365-383; Rainger 1991). And though the biogenetic law is now largely discredited,[125] the idea of relative timing changes occurring in development (heterochrony), thereby resulting in significant evolutionary consequences, can be observed routinely in the work of contemporary paleontologists (McNamara 1990, 1995, 1997). Less attention has been devoted to morphological and paleontological research in the post-synthesis period concerning innovations and novelties because historical studies have focused on the tools rather than problems found in contemporary Evo-devo.

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[125] This is not to say that the philosophical impulse cannot be identified in this period (Delsol 1977) or in the present (cf. Davidson, Peterson and Cameron 1995). One can also see the phenomenon of 'flogging a dead horse' in discussions from this period (e.g. de Beer and Swinton 1958).

We begin surveying the landscape of biological journals from 1935-1980 regarding explanations of innovation and novelty with exemplars chosen by Mayr.[126] First, Mayr highlights the functional morphological investigation of Bock on the origin of avian jaw articulation (Bock 1959). Bock's study of the functional morphology of double jaw articulation illustrated Mayr's point that the transfer of function for the origin of novelty can take place in the presence of a structural duplicate (Mayr 1960, 362). Bock attempted to account for the secondary basitemporal articulation in the avian mandible (the medial brace) that prevents the jaw from disarticulating under strong forces during feeding activity (such as skimming for fish). The concept of *preadaptation* plays a central role in Bock's argument: "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, 201). Bony knobs on the basitemporal plate, which served as attachment points for cervical muscles, were preadapted for the secondary articulation of the medial brace due to their position and projection with respect to the entire basitemporal plate. Bock's research also demonstrates that the study of evolutionary novelty is a natural point of intersection for morphological and developmental research perspectives because he appeals to Schmalhausen's theory of stabilizing selection (Schmalhausen 1986 [1949]) to account for how the jaw articulation could have arisen non-genetically and later been brought under genetic control during ontogeny.

A second set of examples Mayr seized on concerned tetrapod origins and the origin of the tetrapod limb (Jarvik 1955; Løvtrup 1977; Maderson 1967; Romer 1958; Szarski 1977; Watson

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[126] I have limited my focus to English language journals and researchers. There are morphological and paleontological perspectives elsewhere (e.g. Germany), which are critical roots for contemporary Evo-devo (Riedl 1977, 1978; Schindewolf 1993 [1950]; cf. Wagner and Laubichler 2004). I also am not offering an *exhaustive* survey, often citing only a representative article or book by a particular author.

1926; Westoll 1943a, 1943b). This is a persistent topic of conversation as evidenced by numerous notes and comment pieces in journals (Cowles 1958a; Ewer 1955; Goin and Goin 1956; Gunter 1956; Holman 1969; Inger 1957; Orton 1954; Warburton and Denman 1961). Besides the limb, discussions of other distinctive characters that mark the different tetrapod classes are identifiable, such as for amphibians (Estes 1965; Fox 1959; Gans and Parsons 1966; Schmalhausen 1968; Szarski 1957, 1962, 1968), reptiles (Hotton 1960; Kemp 1972; Peabody 1951; Romer 1957; Tihen 1960; Walker 1964), birds (Galton 1970; Troxell 1939; Tucker 1938),[127] and mammals (Hopson and Crompton 1969; Olson 1966). Related to these discussions are an understanding of the comparative anatomy and evolutionary trajectories in fishes (Hoff 1944; Moy-Thomas 1938; Nursall 1962b; Romer 1946; Westoll 1958).

The origin of mammalian features (especially those defining higher categories) constitutes the final genre of examples Mayr chose to deploy (Hopson and Crompton 1969; Olson 1959, 1966), especially the inner ear (Hotton 1960; Tumarkin 1955; Watson 1953). With respect to the origin of the mammals themselves, hypotheses concerning locomotion and physiology (Bakker 1971), reproductive strategies (Hopson 1973; Long 1969, 1972), or particular skeletal elements in the skull (Barghusen and Hopson 1970) were put forward. Morphological and paleontological analyses were executed with respect to the origins of proboscideans (Osborn 1936, 1942),[128] whales (Van Valen 1968), ungulates (Radinsky 1966; Schaeffer 1948; Van Valen 1971), rodents (Wilson 1951), and primates (Gregory 1930, 1935b). Developmental studies were used to argue for the possible origin of higher taxa in several cases,

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[127] Recalling the discussion in chapter 3 about distinguishing questions of the origin of birds from the origin of feathers and flight, it is instructive to observe how this was not done previously. "In a study of [bird origins], which deals so intimately with bird-ancestry, it is inevitable that one be concerned with the origin of feathers, of flight and of other such things that seem to be so essentially a part of bird make-up" (Troxell 1939, 265).

[128] Osborn developed his principle of aristogenesis, which was intended to provide a general explanation of the origin of evolutionary novelties through an appeal to germline potentiality, out of these studies in conjunction with his earlier work on large mammalian species (Osborn 1933, 1934; cf. Rainger 1991).

such as in the external cheek pouches of geomyoid rodents (Long 1976; cf. Brylski and Hall 1988) or mammary glands (Long 1969, 1972).

Invertebrate innovations and novelties were not utilized by Mayr as extensively, though they were readily available (e.g. Barnes 1980; Hyman 1940-1967; Manton 1953; Marcus 1958; Snodgrass 1935, 1965 [1952]). Numerous studies concerned the origin of metazoans and phyla (Boyden 1953; Clark 1964, 1979; Ford 1979; Greenberg 1959; Hand 1959; Hanson 1958, 1977; House 1979; Marcus 1958; Nursall 1962a), as well as the origin of vertebrates from an ancestral invertebrate stock (Berrill 1955; Dillon 1965; Gregory 1946; Jefferies 1979; Løvtrup 1977; Needham *et al.* 1932; Stanley-Jones 1956). Several studies on mollusk origination and evolution were published throughout this period (Brace 1977; Eagar 1977; Holland 1979; Morris 1979; Vagvolgyi 1967; Yochelson 1979). Arthropods were a favorite subject of study, whether the origin of the group itself (Anderson 1973; Cisne 1974; Manton 1949; Manton and Harding 1964), its major subdivisions (Manton 1977), such as crustaceans (Anderson 1969; Garstang and Gurney 1938; Thistle and Hessler 1976), or particular defining features such as castes in social insects (Gregg 1942). Some attention was given to wing origination in insects (Forbes 1943), including by Goldschmidt (Goldschmidt 1945). Studies of annelid groups were also readily available (Anderson 1959, 1966a, 1966b; Clark 1964).

Other attempts to explain evolutionary innovations and novelties from various disciplinary perspectives can be identified. Cowles argued from a physiological standpoint for the origin of fur and feathers based on claims about the heat sensitivity of archosaurs and the need to retard the absorption of solar radiation, rather than as a response to falling temperatures with the concomitant need for better thermo-insulation (Cowles 1939, 1940, 1948, 1958b; cf. Pike 1930). At the molecular level, one can find nascent discussions of biochemical and cytological innovations and novelties (Cohen 1963; Granick 1953; Horowitz 1945; Levy and Levin 1971), including the origin of gene structure and function (Zuckerkandl 1975; Zuckerkandl and Pauling 1962, 1965a, 1965b), chromosomes (Gabriel 1960), eukaryotic cell and organelles (Alsopp 1969; Margulis 1970, 1971; Taylor 1979), and viruses (Northrop 1958).[129] One of the most prominent discussions concerns the origin of chromosomal structures in plants (Barber 1940; Bloom 1977; Jensen 1942; Kimura 1962).[130] Another perennial topic is the origin of sex itself (Dougherty 1955; Williams 1975).

4.3.2. Anachronism, Thematic Observations, and Historical Correctives

These exemplars return us to the difficulty of translating the language of the present (the problem agenda of innovation and novelty) and that of the past (the origin of higher taxonomic categories or major transformations). A good place to observe the translation of past terminology concerning the origin of higher categories into contemporary terminology about innovation and novelty is in a discussion of amphibian skeletal novelties (Orton 1955). In addition to the title of the article ('The role of ontogeny in systematics and evolution'), the following passage illustrates the persistent ambiguity between origin of new groups/categories and the origin of novel characters.

> De Beer (1951) discussed in detail the potential importance of ontogenetic changes and cited examples of various kinds of developmental modifications that might have significant evolutionary results. He treated at considerable length the idea of origin of new major groups by neoteny from highly evolved larvae. It has been speculated that even the chordates may have originated by neoteny; the notochord and somites may have

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[129] Molecular studies were also used to establish phylogenetic junctures, such as immunological data on rates of enzyme evolution for the origin and diversification of salamanders (Salthe and Kaplan 1966).

[130] For the most part I am bypassing discussions of evolutionary innovation and novelty in plants (Berry 1945; Campbell 1930; Chamberlain 1925; Cockerell 1935; Jeffrey 1925a; Jong and Burtt 1975; Just 1948; Lewis 1980; Mehra 1957a, 1957b; Ornduff 1966; Pincher 1935; Popov 1958; Stebbins 1950, 1958; Stidd 1980; Wilson 1942). These studies usually have a morphological and/or embryological orientation, often including paleobotany.

> been larval specializations in the ancestral stock (see Gregory, 1946, 1951; de Beer, 1951). Neoteny is, however, not the only means by which developmental modifications may have major evolutionary consequences. The entire ontogeny as a unit may shift relatively rapidly (in geological time) to a new structural plan. It has been suggested that a change of this nature, the extreme shortening of the vertebral column in both larva and adult, precipitated the origin of the frogs (Orton 1955, 81).

Studies used ontogeny to simultaneously address ancestor-descendant relationships and the origin of innovations and novelties characteristic of taxonomic groups (e.g. Fox 1959). Simpson reviewed an array of outstanding issues in vertebrate paleontology in the early 1960s noting that the "greatest interest attaches to major transformations that are involved also in important problems of systematics and of evolutionary theory" (Simpson 1961, 1681), citing tetrapod and mammalian origins as primary examples. The pervasiveness of this interconnection is seen in a symposium entitled 'The Origin of Higher Levels of Organization' (Bock 1965; Devillers 1965; Hecht 1965; Olson 1965; Schaeffer 1965; Schaeffer and Hecht 1965; von Wahlert 1965): "The purpose of this symposium is to examine the mechanisms of trans-specific evolution through experimental evidence and neontological plus paleontological data. The contributors are concerned primarily with how microevolutionary changes can bring about the major modifications associated with higher levels" (Schaeffer and Hecht 1965, 248).

The issue of translation leads us into another key observation about past explanations of innovation and novelty; namely, their intimate relation to problems of classification from the domain of systematics. Comparative embryology was an especially favored tool for reconstructing relationships among higher taxa, especially those without reliable fossilization (Clark 1979; Hand 1959; Hanson 1958; Marcus 1958). The coalescence of classificatory practice into a distinct discipline under a mostly unified theory of cladistics (Hull 1988b; Mishler 2003; Telford and Budd 2003) fundamentally altered the role of comparative embryology, morphology, and paleontology in phylogenetic investigation, which had included as a core theme the juxtaposition of evolution and development (Amundson 2002; Bowler 1996; cf. Anderson 1973; Berrill 1955). But phylogeny was not necessarily *the* research goal in these disciplines. In a discussion of the coelom and segmentation in metazoans, Clark states in the preface that

> This book is not intended as a direct contribution to the debate on metazoan phylogeny and so I have not attempted to construct phylogenetic trees or to discuss in detail the interrelationships of existing animals. Instead, I have considered some of the principles of comparative morphology which must be taken into account when phylogenies are proposed, but which have hitherto escaped serious discussion in this context. … I have therefore been more concerned with the gross structural organization of animals than with the minutiae which are very properly the preoccupation of systematists who have been the chief contributors to phylogenetic studies in recent years (Clark 1964).

The goal is primarily functional morphology in Clark's case,[131] and in many of these other discussions, with phylogeny being an interesting but subsidiary consideration (cf. Manton 1953, 1977; Manton and Harding 1964).

Although the details found in each of these explanations of evolutionary innovation and novelty cannot be elucidated, we can isolate themes running throughout many of these papers. One prominent thread is the need for morphologists and paleontologists to consider development: "the morphologist should consider the developmental processes that have contributed to the formation of the adult, and not be content merely to compare the resulting forms without reference to these" (Moy-Thomas 1938, 305). The nature of larval stages and metamorphosis were a part of the developmental processes considered relevant to explaining the origin of higher taxonomic groups (Garstang and Gurney 1938; Szarski 1957, 1962). Embryological data are interwoven routinely with functional morphology and paleontological analysis, such as in explaining the origin of the astragalus in reptiles (Peabody 1951), the origin of the vertebrate inner ear (Tumarkin 1955), alterations in the mantle of gastropods (Brace

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[131] "Movement and the relationship between the organism and the physical world appear to have been important determinants of structure and for this reason I have directed my attention particularly to the dynamic and mechanical aspects of animals of different grades of structural organization" (Clark 1964, preface).

1977), coelomic segmentation in mollusks (Vagvolgyi 1967), and hydrocoel formation in deuterostomes (Dillon 1965). Westoll criticized explanations of the origin of the tetrapod limb that did not take into account all of the developmental data (Westoll 1943b). Devillers marshaled developmental evidence for morphogenetic mechanisms potentially involved in three different evolutionary transitions: the origin of the cerebral inductor complex, the origin of paired fins and skull bone variation in fishes, and digit/fibula reduction in tetrapods (Devillers 1965).[132] Lewis and Holder explicitly focus on limb development mechanisms in the chick embryo to broach the evolution of the tetrapod limb (Lewis and Holder 1977), whereas Frazzetta argued for a 'saltational' origin of the moveable joint subdividing the maxilla in bolyerine snakes using functional morphology and phenotypic plasticity considerations (Frazzetta, 1970; cf. Dullemeijer 1974, 1981; Frazzetta 1975).

Besides the prominent feature of classificatory aspirations arising from the interconnection of the origin of evolutionary novelties and higher taxonomic categories, another theme is a focus on structure over function. In part this is natural for paleontological studies but the bias is particularly pronounced. Very few studies directly address the origin of a function except in coordination with particular structures, which is one of the reasons why preadaptation plays a key role in many of these explanations (Bock 1959).[133] Identifiable studies of evolutionary innovations are disparate: drosophilids ovipositing into land crabs that serve as the site of parasitic larval development (Carson 1974), pollen feeding in butterflies (Gilbert 1972), different forms of herbivorous digestion in ungulates (Janis 1976), constriction in snakes (Greene and Burghardt 1978), electric organs in fish (Lissman 1958), slavery in ant communities (Wilson

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[132] Besides development, there are appeals to hybridization or symbiosis for the origin of species and higher taxa (Cuellar 1974; Jeffrey 1925b; Nabours 1930; Stebbins 1958; Taylor 1979; Turner, Brett and Miller 1980).

[133] Preadaptation does not logically require a prioritization of structure, as a function could be preadapted for another function. But, in general, it is not used this way (cf. Wilson 1975).

1975), the carotid sinus reflex in mammals (Lutz and Wyman 1932), the jumping mechanism in frogs (Gans and Parsons 1966), and mating behavior in spiders (Alexander and Ewer 1957), as well as avian flight (Ostrom 1974). Whether or not this represents a *necessary* methodological bias is debatable (Dullemeijer 1974, 1981).

Focusing on the time period that is often seen as the 'golden age' of the Modern Synthesis (including its 'exclusion' of embryology) is particularly instructive since the activity centered on explaining innovation and novelty helps puncture the problematic notion of 'quiescent periods' or gaps in the history pertaining to Evo-devo (Arthur 1997, 2004b; Hall 2004). Articles from this period point toward a strikingly contemporary Evo-devo research agenda. It is also inaccurate to say that the studies undertaken by comparative embryologists, morphologists, and paleontologists were 'out of touch with contemporary priorities' (Bowler 1996) or that they only provided 'classical evidence of evolutionary patterns' (Arthur 1997, cf. Figure 1). They were located in places such as the journal *Evolution*, where the position of the Modern Synthesis was most prominent (Cain 1994). The research is usually not 'genetic' in nature but does focus on mechanisms in evolution and development, not just phylogeny. The main disjunction appears to be disciplinary—disciplines currently prominent in Evo-devo (e.g. molecular developmental genetics) were not at the center of these studies of innovation and novelty as were the disciplines of functional morphology, paleontology, and comparative embryology. The only article approaching a modern genetic strategy to evolutionary novelties was a programmatic piece on the possible roles of repetitive DNA sequence and gene regulation (Britten and Davidson 1971). Comparative anatomical or embryological approaches to phylogenetic relationships were also still present long after their supposed heyday (cf. Bowler 1996). The centrality of systematics in studies of evolutionary innovation and novelty is reflected in the equivocation between the origin of higher taxonomic categories and the features used to designate those categories.

Having now observed the general outlines of research into evolutionary innovations and novelties during this period, we turn to extended analyses of different researchers representing each of the three disciplinary foci identified: comparative embryology (Section 4.4; N.J. Berrill), morphology (Section 4.5; D.D. Davis), and paleontology (Section 4.6; W.K. Gregory).

4.4. N.J. Berrill and the Evolutionary Developmental Biology of Ascidians

Many investigations of the origin of evolutionary innovations and novelties found their home in non-genetic comparative evolutionary embryology rather than experimental embryology. It is natural to turn to Norman John ('Jack') Berrill (1903-1996) when trying to understand this disciplinary contribution. N.J. Berrill carried out a comparative program of investigation on ascidian embryos in the 1920s-1940s in which there is a considerable component that resonates with modern Evo-devo research. In tracing what he perceived as history relevant to a discussion of the intersection between evolution and development in an introductory textbook, Berrill states that

> Soon after the publication of Darwin's *Origin of Species* and its general acceptance by the scientific world of the day, the discovery was made by the Russian embryologist Kowalevsky that the sessile ascidians, previously classed with the filter-feeding, bivalve mollusks, produced larvae that were unmistakably of a chordate character, with a swimming tail complete with notochord and dorsal, tubular spinal cord, and muscle tissue along each side. The conclusion was that ascidians has descended from free-swimming chordate ancestors in the distant past and retained the tadpolelike chordate larvae as a relic thereof. The discovery launched a general investigation into the life cycles of animals in the belief that the life histories represented in a condensed form the evolutionary history of the species or class (Berrill 1966, 714).

Berrill's aim in this section entitled 'Evolution and Development' reminds us that the relationship between evolution and development is not primarily about recapitulation. Before describing neoteny and relative growth ('developmental phenomena that have played a significant part in adaptation and evolution') he made a remark that appears prescient from our vantage point. "A question arises concerning to what extent, if any, the course of development sheds light on the evolutionary past of the particular species. At one time it was thought to throw a great deal, but now not very much. The truth may lie between" (Berrill 1966, 714).

Another reason for reviewing the work of Berrill follows from its high profile role in de Beer's oft-cited and influential synthesis, *Embryos and Ancestors* (de Beer 1958). Berrill's work receives three prominent mentions. In his chapter 'Heterochrony', de Beer cites Berrill's studies on lower chordates that provided a mechanism for increase in size by slippage in the number of cell division cycles relative to gastrulation to get the larger basic vertebrate embryo from a tiny ascidian (see below). In his review of theories on the origin of vertebrates, de Beer draws attention to Berrill's knowledge of larval adaptation and marine ecology in tracking this key evolutionary juncture and rejecting spurious speculations. Finally, in conjunction with the discussion of recapitulation, Berrill is cited for emphasizing that the repetition of ancestral features in the development of descendants does not imply a biogenetic law for phylogenetic reconstruction but signals that these repeated stages or features likely are of special importance for understanding the evolution and development of the concerned lineages. An ideal place to observe these themes is in Berrill's studies of tunicate development in the *Philosophical Transactions of the Royal Society of London* (Berrill 1930, 1931, 1935a, 1935b, 1936).[134]

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[134] Tunicates are marine dwelling members of the phylum Chordata, sharing a notochord, dorsal hollow nerve cord, and paired lateral pharynx slits, and consist of three classes under the subphylum designation Urochordata (Stocker 2001). Their name is derived from the sack-like tunics (largely cellulose based) that enclose the bodies of these organisms. Of the three classes (Thaliacea, Larvacea, and Ascidiacea), the first two are pelagic swimmers

4.4.1. Studies of Tunicate Development

Together, Berrill's five tunicate papers are 256 pages long. He provides his own descriptive embryology of many new species, as well as an evaluation of previous researcher's descriptions (more than one hundred different species combined by his count), in order to make phylogenetic claims about taxonomic relationships and mechanistic claims about developmental changes in the evolutionary transitions among the different morphologies identified. Included in the descriptive portions are detailed camera lucida based drawings. Part 1 tackles the 'simple' ascidians from a 'functional viewpoint' and attends to the 'typical' development found within this group (Berrill 1930). By 'functional' Berrill means the reasons why particular embryological features are beneficial in the ontogenetic environment, such as egg flotation or hatching mechanisms.[135] These features are elucidated through temperature and chemical manipulation of the developmental milieu, such as the addition of gum arabic or pH alterations. Berrill is careful to highlight variation throughout his descriptions of ontogeny, such as in egg size and perivitelline structures.[136] He traces overall developmental variability to the length of time an egg is in the oviduct and the physiological condition of the parent (Berrill 1930, 73). Another important aspect of this work is its taxonomic density. Berrill describes the ontogeny of

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throughout their life history whereas the Ascidiacea are benthic and sessile as adults. The latter are commonly known as 'sea squirts' because of the mechanical ejection of water they release when stimulated. They are found in every ocean and attach themselves to sand or rock substrates, as well as various manmade structures. Ascidians can be either solitary or colonial in organization, of which the latter can be further subdivided into social (asexually cloned and anchored in common) or compound (asexually cloned and wholly enshrouded by a single matrix or test). They filter feed through a pharyngeal basket occupying the majority of their internal cavity. Historically, ascidians were considered an ancient vertebrate ancestor by Darwin (Darwin 1981 [1871], 205-6), following the embryological work of Kowalevsky (Adams 1973; Brauckmann and Gilbert 2004; Mikhailov and Gilbert 2002), and served as a source for discussing the origin of chordate features via neoteny in the 20th century (Garstang 1928).

[135] "The perivitelline space and the outer follicle cells are important from the point of view of the flotation of the egg in that they lessen the specific gravity of the egg as a whole" (Berrill 1930, 41).

[136] "When the development of a large number of eggs is followed, the variability within a batch from one individual, or between batches from different individuals, becomes very striking" (Berrill 1930, 73).

over fifty different species. At several points he rationalizes his choice of organisms to describe based on what groups have not been previously investigated.

One intriguing facet of his developmental studies is a preference for explanations in terms of mechanical causes or using mechanical analogies. For example, in discussing the turgidity of notochord cells, he claims that,

> [i]t seems probable then that the correlated increase in volume of individuals cells, assuming they be contained within a relatively non-elastic cylinder, i.e., of mesoderm and ectoderm, is sufficient to account for the sliding movements and interdigitation described… Probably, however, the notochord possesses a mechanical influence alone, in stretching the muscle cells and stimulating the cells of the ectoderm to divide, for the amphibian 'organiser' has a much more subtle influence, which is definitely non-mechanical (Berrill 1930, 47, 49).

A pervasive influence of D'Arcy Thompson can be seen in these kinds of mechanical explanations of ontogeny and especially in the invitation to contribute to a *festschrift* for him (Berrill 1945). In this piece Berrill uses the tunicate studies to draw out "whether much of the developmental course of an organism may be interpreted as an expression of latent organization progressively sanctioned by successive expansions [of volume]" (231). It is here that his proclivity to comprehend development in mechanical terms is most evident.

> The whole progression of development may be described as a protoplasmic sheet expanding three-dimensionally as a hollow sphere from which almost entirely by foldings, invaginations, and evaginations develops the complexity of the compartments, structures, organs, and systems that is the functional organism. That the course of development *can* be so described, even in outline, is some indication of its simplicity and directness (234).

Berrill's use of mechanical descriptions for understanding ontogenetic processes is significant because it partly explains his hesitancy in attributing the causal generation of this form to genetic factors alone (see below).

The second installment on tunicates sets out his account of the abbreviation of development in the family Molgulidae from the simple ascidians (Berrill 1931). This family provides a robust case study for the roles of viviparity and yolk accumulation on the truncation of ontogenetic processes, phenomena now more commonly collected under the term 'direct development' (Hanken 2003). Berrill discusses the four logical combinations of reproductive mode (oviparous versus viviparous) and type of development (urodele [indirect] versus anural [direct] development). He held that oviparous, indirect development was the ancestral character state and attempted to detail putative mechanistic ('how') and 'teleological' ('why' - selection) reasons for these transformations. This involved a subtle deployment of knowledge concerning marine larval ecology of the different species. Berrill argued that the distinct habitat of Molgulids (sand, mud, or shell gravel) encourages most of them to live unattached (in contrast to other ascidians). The tadpole larval stage is primarily involved in site selection for permanent anchorage, thus giving a selective rationale for the loss of this stage in the anural Molgulids. In terms of developmental mechanics, mechanical explanations are on display.[137] Using these distinct lines of reasoning, he becomes convinced that direct development has arisen independently multiple times in different ascidian lineages. Again, the work is marked by taxonomic density (twelve new Molgulidae described).

Part 3 is a thorough exploration of differential retardation and acceleration in development, i.e. heterochrony (Berrill 1935a). Berrill focused on the origin of viviparity, which he attributed to the relative shortening of the oviduct, while concentrating on the significance of cell size and yolk accumulation during this transition. The identification of relatively constant cell size among ascidians drove him to see any variation in embryonic stage or adult size as

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[137] "Therefore, the whole of the dissimilarity existing between anural and urodele development can be explained if the notochordal cells fail to swell, and consequently fail to commence the sliding and interdigitating process, and this is believed to be the true explanation" (Berrill 1931, 327).

rooted in varying cell number. This kind of reasoning was foundational for his account of the origin of vertebrates (see below). Figure 4 gives a taste of these comparative embryological studies through a complex visualization of developmental sequence and stage information, especially with respect to correlations in the acceleration and retardation of developmental timing for different ontogenetic events among various ascidian species.

Part 4 turns to the phenomenon of asexual reproduction via budding, exploring the compound ascidians more directly while trying to draw out generalizations regarding the morphology, morphogenetic processes, and histological properties of budding (Berrill 1935b). Ongoing asexual budding permits additional experimental observations on morphogenesis besides the primary embryo to adult trajectory. Part 5 attempts to "trace the probable course of evolution within ascidians" with particular attention to the heart, pericardium, and epicardium, primarily because of the purported link of the first two with vertebrate morphology (Berrill 1936). Berrill thought *Ciona* to be most representative of the ancestral ascidian form (cf. Dehal *et al.* 2002). The comprehensive nature of these papers and other work by Berrill led to an invitation from the Ray Society to produce a monograph on the Tunicata with special reference to British species (Berrill 1950). It is likely that no one knew as much about tunicates as Berrill by mid-century and, because of his taxonomic breadth, no one has ever attained to his breadth and depth of knowledge for the entire group.

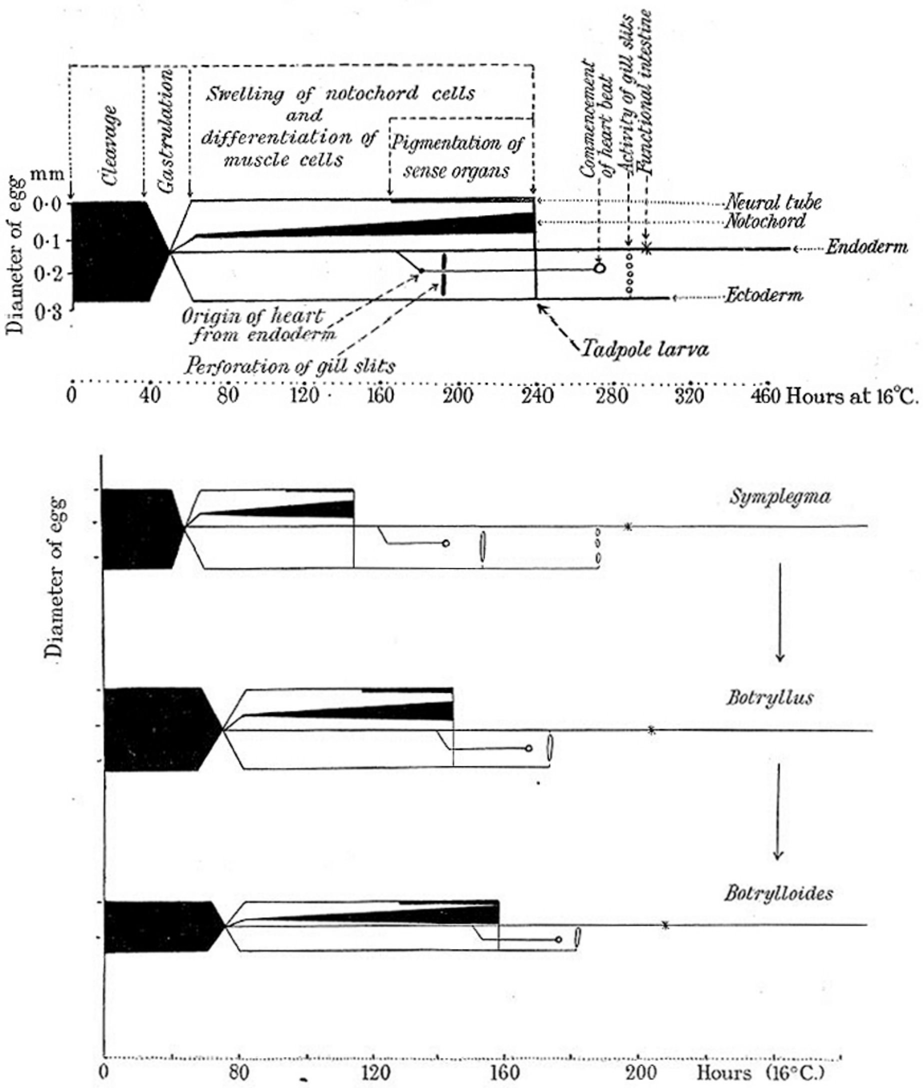

Figure 4: Berrill's Diagrammatic Representation of Developmental Events and their Relative Timing in Different Species

The top panel, based on the ontogeny of *Clavelina lepadiformis* at 16°C, is the key to understanding the features of the bottom panel graphs, which in Berrill's estimation constitutes a genuine phyletic series through decrease in egg size and retardation of ontogenetic events in the direction of the arrows (Berrill 1935a, 303, 322).

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4.4.2. Explaining the Origin of Vertebrates

One of the thorniest topics in historical biology is accounting for the origin of key vertebrate characters. This investigation exercised a variety of researchers in the late 19th and early 20th centuries (Bowler 1996, ch. 4; Gans and Northcutt 1983; Holland and Chen 2001; Northcutt and Gans 1983). Many are aware of Garstang's work because he was pivotal in the downfall of the biogenetic law (Gould 1977). His paper "The Morphology of the Tunicata, and its bearing on the Phylogeny of the Chordata" advanced the thesis that a primitive chordate tadpole could be derived through a variety of alterations in developmental timing (e.g. paedomorphosis - adultation of larval form) from a echinoderm-like larval ancestor (Garstang 1928).[138] These concern the problem agenda of innovation and novelty in the terminology of the origin of key features defining higher taxa (cf. Section 4.3). Berrill attempted to synthesize his tunicate studies as a platform for explaining vertebrate origins (Berrill 1955).

Berrill began by reviewing major discarded theories of vertebrate origins (annelid, arthropod, and echinoderm) before turning to highlight the main controversies over tunicates, amphioxus, and other 'protochordates' as vertebrate ancestral candidates. He explicitly employs developmental data to reject recapitulatory evolutionary conclusions (chapter 9). These lessons on the intersection of evolution and development occur elsewhere in his writings.[139] This

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[138] Recent investigations of the origin of vertebrates have tended to prefer cephalochordate models such as amphioxus (Holland 2002; Holland and Holland 2001; Holland and Chen 2001), in direct contrast to Garstang's conclusion that amphioxus was an offshoot of the lineage that eventually produced the tunicates. "The ascidian tadpole is much too specialized to have provided an evolutionary ancestry for the vertebrates" (Stocker 2001). This shift also coincides with an ignoring of Berrill's research.

[139] "Indirect development has been the basis for much of the supposed support for the theory of recapitulation, mainly because transformations from one kind of organism to another during an individual life cycle have the appearance of a progressive evolutionary change. But because of the pressure of natural selection operating at all stages of development, the retention of a more or less ancestral form as a larval stage in development is only one of several possibilities. During the evolution of a particular group of animals, progressive change or adaptation may have consisted mainly in increase in the size of the fully adult stage, together with whatever internal adaptations may have been necessary to maintain the metabolic, functional, and structural efficiency of the organism. Or the adult

negative assessment of recapitulation contrasts with a strong statement of the importance of development for understanding evolution.

> It is essential, I think, to understand how an organism, vertebrate or otherwise, develops, if we are to understand much concerning its evolution; for every individual organism develops as a whole and not in bits and pieces, and while we are inclined to think of mutational changes either in terms of genes and chromosomes or of adult character, the effective innovations are essentially small changes in the nature of early developmental processes of growth or organization (Berrill 1955, 6-7).

Garstang's hypothesis for the origin of vertebrates from a tunicate-like ancestor via paedomorphosis constituted the theoretical context with which Berrill began his tunicate studies.[140] Berrill agrees on the tunicate-like nature of the chordate ancestral lineage but is convinced that the actual changes occurred in a different fashion.

> On [Garstang's] theory the ascidian tadpole becomes essentially an interpolation in the ascidian life cycle; and by suppression of metamorphosis and through further evolution it gives rise to the vertebrates as a whole. This is the general thesis, with which I am in agreement, although not with the manner in which Garstang supposes the changes to have taken place" (Berrill 1955, 9).

Garstang held that (1) ascidians evolved from organisms in the hemichordate class Pterobranchia; (2) the tadpole larva evolved from larvae similar to echinoderm dipleurula and enteropneust (another hemichordate class) tornaria, which accounts for a prolonged free swimming phase and yolk accumulation; and, subsequent to (1) and (2), (3) muscular segmentation was acquired and facilitated the emergence of a neotenous chordate morphology. Berrill rejects (1) and (2) on the basis of fossil echinoderm forms, his own knowledge of ascidians and their larval ecology, and chalks up the similarities to convergence.

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state may have persisted essentially unchanged but new adaptive forms may have been interpolated at an earlier stage of the life cycle. Or little that is new has appeared either with regard to bigger and better end products or with regard to novelties at various earlier stages, but the whole developmental procedure whereby an egg develops and grows to form the adult organisms may become streamlined, with shortcuts and increased efficiency in developmental processes occurring throughout" (Berrill 1971, 188).

[140] In retrospect, Berrill claims he chose ascidians because no else was paying attention to them (Berrill 1983, 948).

> It does not seem reasonable, therefore, to trace evolutionary connexions along a path that leads from a highly specialized and differentiated larval form of certain species or genera of one phylum to equally specialized larvae restricted to only certain members of another phylum, although what appears to be unreasonable is not necessarily impossible (Berrill 1955, 41).

The ultimate irony, given Garstang's own role in arguing against Haeckelian interpretations of development, is that in Berrill's estimation Garstang's error is an implicit form of recapitulationism! The alternative to Garstang's thesis about the gradual origin of the tadpole larvae is that it be considered a 'developmental innovation' with immediate selective value. This hypothesis demands attention to developmental dynamics, something lacking in Garstang's account. Chapter 7 ('Developmental Analysis of the Ascidian Tadpole and the Question of its Origin') provides this perspective, again drawing on Berrill's detailed tunicate studies.

Although Berrill was careful to canvas issues of homology for a variety of morphological features at stake in the debate, he explicitly offered a developmental mechanics explanation of the transition. He attempted to explain the origin of vertebrates via a mechanism of size increase by slippage in the number of cell division cycles relative to gastrulation to get a larger basic vertebrate embryo from a tiny neotenous ascidian larval form. This goes back to his insight that size variability in ascidians was not due to cell size but cell number. Thus, if you increase the number of cell divisions prior to gastrulation (either by accelerated cell division or retardation of the onset of gastrulation), the total number of cells dramatically increases. Support for this comes from comparative studies showing that ascidians have 5-7 pre-gastrulation cleavages and less than 100 cells whereas lampreys and newts have 11 or more pre-gastrulation cleavages and 2,500-16,000 cells. Another line of evidence comes from notochord cell number, which appears to be the 'pacemaker' of ascidian ontogeny regardless of egg size (always 40-42 cells). Lamprey notochords contain ~500 cells and newt notochords ~1,200 cells.

These mechanistic themes are generalized when discussing the evolution of development.

> Accordingly in virtually every group of animals we find kinds which, mainly through great increase in egg size and yolk content, have eliminated not only whatever functional larval form might once have been present but, necessarily, whatever embryonic and prepattern stages led to larva formation. In such cases traces or rudiments of vanished structures may persist; where they are recognizable they have at times been interpreted as evidence for a condensed recapitulation of the evolution of the species. But the probability is that such remnants have persisted by virtue of their importance in the developmental construction process (Berrill 1971, 190).

Berrill's aim is not phylogenetic reconstruction but a mechanistic explanation of an evolutionary novelty. Additionally, he was careful to detail the ecological conditions conducive to these ontogenetic changes. For example, the increased size due to an alteration in cell division cycles producing a larger embryonic form would have allowed for greater migration capability, especially into fresh water habitats, to exploit novel feeding resources. Berrill supported this capability by showing that an increased length of tadpole for different ascidian species led to an overall increase in speed and decrease in the number of tail strokes per second.

Berrill's use of developmental data for conclusions regarding the origin of evolutionary novelties is significant because it shows how combined attention to ecology, development, and evolution were being used to study more than phylogenetic questions during the mid-20th century: "to envisage each step of the [evolutionarily] transforming organisms in terms both of their embryological development and in relation to their environment" (Berrill 1955, 10). As he noted later in life: "A general pattern of chordate and nonchordate larvae appeared, relating to environmental selection and a seemingly very simply mutational change in developmental mechanics" (Berrill 1983, 948). This ecological component is something not often recognized in considering comparative embryological hypotheses of individuals like Berrill. The primary criterion is not the ability to imagine the morphological transformations but rather to give an immediate selective benefit account for any of the transitional forms *and* the developmental mechanics necessary for those changes. Before we ever get to an evaluation of Garstang's theory, we are treated to multiple chapters on 'the survival value of the ascidian tadpole' and 'comparative larval ecology', all of which is drawn directly out of his studies from the 1930s. The feature emphasized by Berrill is that the ascidian tadpole is a *derived* feature (favored due to site-selection for adult anchorage), which evolved in the ancestral tunicate lineage and was then co-opted via developmental mechanisms related to cell proliferation for specific ecological advantage to produce the proto-vertebrate characteristics.[141]

I have only scratched the surface of Berrill's discussion in *The Origin of Vertebrates*, which sets out critical aspects of the evolution of other vertebrate structural novelties, such as eyes, fins, bone, jaw and head, as well as the origin of amphioxus. This is done according to a framework similar to that found for the origin of vertebrates. Berrill's book was widely reviewed and warmly received by his scientific peers, though with expected disagreements concerning his main thesis (Carter 1957; Moment 1956; Simpson 1955; Wells 1956).

4.4.3. Conceptual Themes of a Comparative Embryologist

Before turning to our next exemplar, it is necessary to observe Berrill's mature perspective on developmental mechanics because it illuminates the nature of his explanations of evolutionary novelty. Several conceptual themes emerge that condition the types of explanations he is willing to countenance for the origin of evolutionary novelties. Besides the '*contra* recapitulation' theme already dwelt upon, another core thematic element of Berrill's biological

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[141] [T]he tadpole larva exists among ascidians because in the great majority of cases it is vitally necessary for the location of a suitable site for settlement, and not because it is in anyway an inevitable ancestral relic retained in the course of development. It exists because it is needed for the performance of delicately controlled locomotor responses at a critical moment in the life cycle. Where there is no such need, there is usually no tadpole (Berrill 1955, 30).

theorizing is the explanatory insufficiency of genes (and cells), which can be observed in his *Growth, Development, and Pattern* (Berrill 1961) and other places (e.g. Berrill 1971, ch. 8). “Neither cells nor genes, *taken by themselves*, sufficiently account for the development and maintenance of pattern” (Berrill 1961, 2, my emphasis). This putative insufficiency drove him to continue focusing on possible organizing forces such as Child’s axial gradients of structure based on metabolic gradients (Child 1941) or electrical potentials. But both were deficient in Berrill’s eyes because they are overly focused on chemistry and physics. An understanding of the organizing forces at biological levels was needed because “new properties or qualities emerge as the scale of organizational territories increases” (6).

This claim sets the agenda for his discussion in *Growth, Development, and Pattern*: “Such is the aim of this book: to describe the dynamics of development and maintenance of form and structure at a purely biological level of inquiry and in those organisms that best lend themselves to this inquiry” (6). Painstaking case studies of various groups of organisms (including many of the features under developmental genetic focus today, such as flower and leaf meristem, flatworm and hydra regeneration, and arthropod segmentation *inter alia*) are used to slowly build a case for ‘supracellular’ fields of organization as the cues leading to morphological outcomes. The natural question following upon these conclusions is the nature of these fields.

> The basic problem in both cell growth and building construction lies in the planning. Are the cues to which the cells respond in such an orderly way “built in,” within the cells, or are the activating cues supracellular? If the controlling agency is supracellular—as seems likely—what is its material basis? … The question arises: can these various growth phenomena be interpreted in terms of a continuously growing sheet of protoplasmic material lying at the base of the ectoderm and endoderm and determining directly the fate of the adjacent cells and indirectly that of their descendants? … each unit or morphogenetic field seems to consist of a center of activity surrounded by a more vaguely defined and less-active peripheral territory of the same general character. As growth proceeds, the center of each territory expands outward, so that the center commonly retains a relatively high growth rate and remains labile, and the peripheral

> region undergoes a rate of decrement and exhibits differentiation from the margin toward the center (224, 241, 408).

The case for the existence of these fields is strong but the causal question lurks unanswered or postponed most of the time.

Morphogenetic fields are a critical recurring theme in Berrill's work and have received attention within Evo-devo (Gilbert, Opitz and Raff 1996). Gradients and fields were common currency of experimental embryologists throughout the period from 1920-1950 (cf. Theiffry 2001). Berrill's own studies of tunicates, in particular asexual budding (Berrill 1935b), again provide a good chunk of the fodder:

> What controls such orientation patterns? In the organisms under discussion [tunicates] there seems to be an exceptional opportunity to examine morphogenetic activities which apparently override cell individuality, yet seem nonattributable to diffusion or other metabolic gradients (Berrill 1961, 350).

Berrill concludes that much of this activity is the result of intercellular 'cement' or an extracellular matrix, the nature and operation of which is then the outstanding research question arising from his study: "[T]he main theme of this book [is that] the fundamental nature of the continuum itself remains the problem of overwhelming importance to any understanding of organism and organization" (Berrill 1961, 541). In many ways this is the hallmark of Berrill's investigative approach—tackling a question in depth with the primary aim of discovering new important questions to pursue.

A final conceptual theme relevant to Berrill's explanations of evolutionary innovation and novelty is the hierarchical construction of organisms.

> Matter exhibits *levels of organization*, from subatomic particles to atoms, molecules, cells, organisms, and ecosystems. … At each higher level of organization, there is an *emergence* of new properties; in other words, at each level of organization the *whole is more than the sum of its parts*. Matter undergoes processes of *self-assembly*.

> *Development is a multilevel phenomenon*, and during development the organism passes from one level to another (Berrill 1971, 11).

This theme was sharpened by the molecularization of embryology, which Berrill did not perceive as an unalloyed good.

> What is studied in biochemistry, molecular biology, and cell biology is process, mostly chemical. What is missing is attention to spatial organization, what controls it, what determines it, what changes it. There is no adequate theory anywhere in sight (Berrill 1983, 951).

The lack of attention to spatial organization went hand in hand with the inability to move easily between different levels of structural organization. At several points Berrill articulates this perspective as a warning against an overweening preference for 'genetics only' explanations.

> When asking questions of nature, at whatever level, the framing of the question is of the utmost importance, because the answer, if any, will be in the same terms as the question. If the question relates to the role of the genes in development, the answer will further our understanding of that role. If the question relates only to cytoplasmic events during development, something may be discovered concerning those events but little will be learned about related gene activity. In view of the multilevel organization of organisms and the developmental transformations, such limitations need to be kept in mind. Questions and answers related to one level are not likely to illuminate another level, except to raise questions of another kind. The relationship between levels must be in the question if it is to appear in the answer (Berrill 1971, 5).

The reductionism Berrill criticizes concerns inappropriate extrapolation across levels.

> [T]here is a continuing debate between reductionist and organismal biologists concerning the role of molecular biology to biology as a whole. The reductionists adopt the precept that a fuller understanding at the molecular level *will eventually yield explanations of all that happens at higher organizational levels*; organismal biologists believe that the organism as a whole needs to be studied at its own level (Berrill 1971, 6, my emphasis).

Because Berrill was convinced that novel properties emerge at higher levels of organization that are related to but not merely a sum of properties at underlying levels, a purely molecular methodology missed necessary parts of any explanation.

> Even to formulate the problems that [the emergence of novelty and new units of organization] present, the activities and interactions must be studied at their own level if the laws of pattern and order at that level are to be even partially understood. Only then is there a prospect that they can be related to or interpreted in terms of their constituent assemblies (Berrill 1971, 6).

In connection with attention to distinctive features at higher levels of organization is an emphasis on the role of self-organization in biological processes. "The dominant theme is that of self-assembly and directed assembly of organized substance, with molecular and cell biology brought in only to the extent they are needed for the developmental point of view" (Berrill 1971, preface). Therefore any explanation of an evolutionary innovation or novelty must consider properties that arise at higher levels of organization from self-organization: "Development and evolution may both be regarded as a process of attaining successively higher levels of organization of matter by means of self-assembly and directed assembly" (Berrill 1971, 3).

4.5. D. Dwight Davis: Functional Morphology, The Modern Synthesis, and Evolutionary Novelties of the Giant Panda

4.5.1. Morphology and the Modern Synthesis

Elsewhere I have identified three discernable accounts of the relationship of comparative anatomy (or morphology) to the Modern Synthesis (Love 2003a, 2005): (1) covert contribution (Waisbren 1988); (2) potential to contribute without actual contribution; and, (3) theoretical inability to contribute because morphology is descriptive (Coleman 1980; Ghiselin 1980). There are several reasons to favor the second perspective, which preserves the sense of exclusion experienced by morphological researchers during and after the forging of the Modern Synthesis, especially in terms of the problem agenda of innovation and novelty, without imputing intentionality for this result to other researchers.[142] The perception that morphological (and some paleontological) research represented an alternative conception of evolutionary theory not strictly part of the Modern Synthesis implied that these conceptual frameworks were specious.[143]

One point of entry into the process of adjudicating between the second and third historical accounts is to dissect attempts in the American context of the late 1940s to detail a contribution from the ranks of morphology to the synthetic theory of evolution. One possible candidate is D. Dwight Davis. In his report from the 1947 Princeton meeting of the Committee on Common Problems of Genetics, Paleontology, and Systematics, Davis opens with a familiar refrain: "Recent syntheses of current evolutionary thought have, almost without exception, ignored comparative anatomy completely or considered it only very obliquely" (Davis 1949a, 64). He did not explicitly challenge the synthetic theory of evolution in this respect and acknowledged that morphologists had not thought in terms of 'populations' (76). Davis perceived a remarkable congruence of ideas between population geneticists and evolutionary morphologists, and his article offered a picture of morphological research as *consistent* with the aims of other domains within the Modern Synthesis. Despite his claim of a reciprocal relationship between the findings of genetics and morphology, Davis never provides an account of why morphology is important for genetics.

A constructive account of the importance of morphology absent in his 1949 article can be partially recovered in a later discussion (Davis 1960). While delineating the proper goal of comparative anatomy Davis consciously steered clear of what he perceived were idealistic notions found in the phylogenetically oriented morphology of the Gegenbaur School and its

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[142] This is not to say intentional exclusion might not have been operating. Demonstrating the intention to exclude is more difficult than demonstrating the existence or perception of exclusion.

[143] For example, at a Darwin centennial celebration held in Chicago in 1959, the morphologist and paleontologist Everett Olson voiced a worry over being sidelined from the predominant ideas of the synthetic theory of evolution (Olson 1960). See my discussion of his comments elsewhere (Love 2003a, 2005).

conceptual progeny (Laubichler 2003; Nyhart 1995), locating morphology's non-contribution to the Modern Synthesis in transnational obstacles of misunderstanding. Davis believed this occurred in part because the 'subtle' meanings of morphological concepts were hard to grasp outside of the German-speaking context and German anatomists failed to grasp 'key' aspects of Darwinism. Davis was in a position to make these comments because he and his colleague Karl Schmidt had translated the work of German-speaking morphologists into English. For example, they had a draft translation of Adolf Portmann's *Introduction to the Comparative Anatomy of Vertebrates* (1948) ready in 1951. Upon Schmidt's death (September 1957) the University of Michigan press expressed interest in the manuscript, although they ultimately decided against publication. In response to the initial interest in the manuscript, Davis touched on the problems of understanding between American and European morphologists. "I do not believe this book could be published as a straight translation, however thoroughly corrected and polished. As I recall, there are certain viewpoints that would be unacceptable in the U.S. Indeed, the whole book reflects the differences between European and American attitudes toward zoology in general."[144]

Davis rejected the claim that comparative anatomy could not contribute to questions of evolutionary causality largely because morphology addressed *higher levels of organization* inaccessible to genetic approaches, and he advocated shifting the focus of morphologists from structural similarity to structural difference.

> If comparative anatomy is to qualify as a science it must, like any other science, offer a rational explanation for the phenomena with which it deals. The phenomena of comparative anatomy are not the observed structure of vertebrates, but the observed differences between the structure of one vertebrate and another. …its proper goal is …to explain the observed variations in [the common structural] plan (Davis 1960, 46).

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[144] Letter to Edwin Watkins, March 6th, 1958. Field Museum of Natural History Archives, Box 1, Original Zoology, Davis, D. Dwight, MSS. Original and translated works.

‘Major’ differences in the common structural plan attended to by comparative anatomists are based on the same mechanisms as those minor phenotypic variations described by population geneticists. The problem becomes demonstrating how the transitions occurred in a particular case. Morphology contributes to a causal understanding of evolution at a level inaccessible to laboratory genetic studies, illuminating the phenomenon of adaptation at higher levels of structural organization: “we are dealing with adaptation, with functional mechanisms, and differences in structure are meaningless unless they can be correlated with differences in function” (49). After identifying structural differences and correlating these differences with function in relation to organismal habits and behavior, the last step is to figure out whether or not the morphological traits in question are under direct or indirect genetic control. For Davis, this was the way to ‘salvation’ for comparative anatomy (50).

Davis’s argument is still far from complete and does not fully resolve whether morphology had distinct theoretical resources available to contribute to the Modern Synthesis. But there is reason to suppose from Davis’s unpublished papers that these are only glimpses of material that was planned for a book-length treatment. In the same letter to Edwin Watkins about the translation of Portmann, he wrote:

> My personal opinion is that every existing textbook of comparative anatomy is based on concepts of the Nineteenth Century, and therefore cannot be expected to inspire either the student or the teacher of today. A complete re-orientation of approach, consonant with modern biological concepts in other fields, is badly needed. … I started to write what I conceive to be such a text, but I don’t know whether I will ever finish the job.[145]

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[145] Letter to Edwin Watkins, March 6th, 1958. Field Museum of Natural History Archives, Box 1, Original Zoology, Davis, D. Dwight, MSS. Original and translated works.

Samples of this material can be found in a collection of outlines, text, and bibliographies entitled "The Comparative Morphology of Vertebrates."[146] The first section is devoted to a definition of functional morphology (in outline only) where he emphasizes the difference between a static descriptive anatomy and a dynamic comparative anatomy representing a "shift of the major interest fr[om] the product to the process." The second part, "The problem of adaptation" (outline only), reveals that his aim is to understand the "origin of functional adaptations", especially those that mark higher taxonomic categories. ("Adaptation at population [and] subspecies level vs. adaptation at supergeneric level.") The third part, "Locomotion", exists in both outline and as partially completed prose. An assemblage of concerns includes biomechanical constraints alongside an extended discussion of "the question of the origin (*as opposed to the evolution*) of paired appendages" [my emphasis], one of the classic instances of evolutionary novelty.

Another unpublished outline entitled "Animal Locomotion" reinforces these emphases.[147] Of four ways described to study animal locomotion (Phylogeny, Mechanics, Physiology, and Origin of Adaptive Mechanisms), it is clear that Davis is in favor of the latter, which he explicitly notes integrates data from developmental mechanics. Under a heading on evolutionary mechanisms, a sub-point reads, "Pop. Genetics = mech.of evol.at lowest level (Not much help in locomotion problems)." A section follows this on the limitations of genetic experimentation for understanding the origin of suprageneric adaptations. The emerging theme through all of this work is that the theoretical contribution of morphology to evolutionary theory is *analytical tools and conclusions at higher levels of structural organization*. Although his papers favor the

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[146] Not dated. Field Museum of Natural History Archives, Box 1, Original Zoology, Davis, D. Dwight, MSS. Original and translated works.
[147] Not dated. Field Museum of Natural History Archives, Box 1, Original Zoology, Davis, D. Dwight, MSS. Original and translated works.

second historical account that morphology could have contributed to the Modern Synthesis but did not, these comments and Davis's keen interest in evolutionary novelties such as paired limbs and the panda's thumb lend credence to considering him as part of a morphological perspective for history relevant to Evo-devo.

I have previously argued that Davis's agenda for a functional approach to morphology reveals that it was not comparative anatomy *per se* that was excluded from the Modern Synthesis but rather the research perspective of typology often associated with morphology (Love 2003a). Claims by Rainer Zangerl (a vertebrate anatomist who worked on fossil turtles at the University of Chicago) that the 'morphotype', which intentionally abstracts away from existing variation, is where "morphology must and can make an important contribution to the future development of ultimate theoretical thinking in biology" (Zangerl 1948, 372) simply fell outside the pale of Modern Synthesis orthodoxy. Further issues about the Modern Synthesis are ignored here in order to draw attention to the specifics of Davis's work and how it can be considered part of a history relevant for Evo-devo via his interest in evolutionary innovations and novelties. In addition, it helps to fill a gap in our knowledge, because recent historical studies of comparative anatomy and morphology have primarily focused on the period prior to 1940 (cf. Bowler 1996; Maienschein 1991; Nyhart 1995, 2002), and gives insight into a unique locale of biological research. Davis worked at the University of Chicago where a more flexible, but less prominent, theoretical framework for morphology and paleontology quietly continued with individuals like Davis and Everett Olson, laying the foundations for a highly interdisciplinary research context that still exists today (Rainger 1993).

4.5.2. Vertebrate Functional Morphology

Delbert Dwight Davis (1908-1965) was a vertebrate anatomist who became the curator of the Division of Anatomy at Chicago's Field Museum of Natural History in 1941. Although his early work from the 1930s focused on reptiles and amphibians, his interest in mammals (and carnivores in particular) predominated during his tenure as curator. One feature that caught his attention in bears is the distinct scapula with its unusually large postscapular fossa in comparison with other carnivores (Davis 1949b). This unique feature led him to consider its significance because he was interested in understanding the morphological similarities between bears and the giant panda. The task required an investigation of associated muscles and the biomechanics of the shoulder—a functional morphology of the shoulder architecture of bears. After considering distinct facets such as the rectangular shape of the scapula (in contrast to the fan shape in other carnivores) that anchors the needed flexor muscles of the broad neck found in bears, making explicit comparisons with the shoulder flexors of other carnivores, and investigating the relevant biomechanics, Davis identified six distinctive features of the bear shoulder. But none of these features is qualitatively different and thus the unique shoulder architecture of bears contained no structural novelties. "None of these differences is absolute; each is merely a quantitative difference from the normal carnivore condition. There is nothing qualitatively new in the shoulder of the bear" (302). It is an exaggeration of that found in its nearest known relatives, procyonids (e.g. raccoons). Functional study of the relevant structures shows that the form of the shoulder architecture in bears is designed for climbing. This conclusion is reinforced by the convergent aspects of shoulder morphology in anteaters and armadillos adapted for digging.

Davis's study of shoulder architecture in bears was ultimately a prelude to his lifelong interest in the giant panda. Although many know that Davis produced a massive treatise on the panda through the popular writings of Gould (Gould 1980a, 1980c, 1980d), the emphasis on imperfect adaptation and historical contingency in these articles overshadows a key aspect of Davis's investigation, which Gould would have been keenly aware of apart from the moral he sought to impart concerning evolutionary tinkering. Gould exhibited an interest in the evolutionary significance of allometric growth early in his career (Gould 1966). This was later observable in his work on the history and evolutionary importance of heterochrony (Gould 1977). What Gould finds attractive about Davis's discussion of the panda and its unique opposable thumb is the postulation of the enlarged radial sesamoid resulting from a simple mutation "affecting the timing and rate of growth" (Gould 1980c, 23). This was "D'Arcy Thompson's solution of reduction to a simple system of generating factors" such that a complex morphological feature can "arise as a set of automatic consequences following a simple enlargement of the radial sesamoid bone" (Gould 1980a, 43). Revisiting Gould's comments directs us to examine the thematic structure of Davis's investigation of the giant panda.

4.5.3. The Giant Panda and Evolutionary Novelty

Davis's study was originally undertaken in order to determine the taxonomic position of the giant panda (*Ailuropoda melanoleuca*) but, as seen in the title, it expanded into a broad morphological study of evolutionary *mechanisms*.[148] He was working in the functional morphological framework that emphasized the adaptive differences of vertebrate form.

> Comparative anatomists have scarcely begun to seek … adequate explanations for the differences in vertebrate structure. …it is of crucial importance to ask whether comparative anatomy can undertake to explain, in causal-analytical terms, the structural differences that characterize taxa among vertebrates. …[comparative anatomy] must shift

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[148] Published as Volume 3 of *Fieldiana: Zoology Memoirs* by the Chicago Natural History Museum, the 339, 32 centimeter pages of Davis's monograph with lavishly detailed drawings (some in color) is clearly a life's work. I cannot do it full justice here where I focus only on those aspects dealing with explaining evolutionary novelties.

> its major emphasis from the conservative features of evolution to its radical features, from the features that organisms under comparison have in common to those they do not have in common. It must seek rational explanations for these differences, drawing on data from other fields where this is necessary and possible (Davis 1964, 5, 11).

Davis did not attribute any significant morphological change to natural selection operating on the gradual accumulation of small mutations. He held that there was increasing evidence that, "in vertebrates, a quite simple change in epigenetic mechanisms may have a profound and extensively different end result" (5). This prefatory remark in favor of epigenetic mechanisms is expanded into the fourth formal goal of his investigation in the Introduction.

> Determination of the morphogenetic mechanisms that were involved in effecting these changes [in structure]. …By a judicious combination of the comparative method with the known data of mammalian epigenetics I believe it is possible to infer, with varying degrees of confidence, the true mechanisms behind many of the major structural differences that distinguish *Ailuropoda* from the true bears (12).

The Introduction also highlights Davis's acceptance of the importance of relative growth rates (allometry), geometric transformations, and rate genes as he invokes Huxley (Huxley 1993 [1932]) and Thompson (Thompson 1992 [1942]), as well as Richard Goldschmidt's *Physiologische Theorie der Vererbung* (1927).[149]

Davis's analysis of limb proportions in giant pandas and bears demonstrates that they are not immediately explicable via attention to functional requirements. Commensurate with this finding is the discovery of allometry in these proportions (length of tibia vs. length of femur), as well as in the pelvic region (breadth vs. length). Davis compared these intraspecific relative growth plots for giant pandas and different bears interspecifically to draw out principles of

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[149] There are multiple meanings of 'allometry' or different kinds of allometries (Gayon 2000; Gould 1966; Strauss 1993). Here I am using the term broadly to capture the idea of coordinated alterations in morphology due to altered rates of growth during ontogeny with evolutionary implications. The two forms most relevant in the present discussion are the *relative* growth of one part to another or the whole organism (Huxley's *heterogony* or allometry) and *absolute* shape transformations between two different organisms (Thompson's deformed cartesian coordinate maps). These distinctions, and the many interconnections between the work of Huxley, Thompson, and Goldschmidt, are extensively discussed elsewhere (Churchill 1993).

evolutionary change in morphology. "Body proportions in the pandas and bears are not the result of selection for mechanical efficiency. Rather they reflect pleiotropic correlations with other features that have been altered through natural selection" (Davis 1964, 40). The nature of the panda skull in contrast to that of other bears, as well as other carnivores, is elucidated via transformation grids with deformed cartesian coordinates. Davis concludes that *Ailuropoda* and *Ursus* show no critical differences from a generalized carnivore in longitudinal proportions of the skull, although depth and breadth do. Despite the fact that this conclusion only relies on qualitative geometrical considerations (cf. Huxley 1993 [1932], ch. 4), when corrected for the effect of absolute size and supplemented by principles from the biomechanics of mastication (*Ailuropoda* has greater efficiency in this respect than a generalized carnivore), the differences in skull proportion can be attributed to increased herbivory among carnivores, exhibited to an extreme in the giant panda (Davis 1964, 67-69). The panda skull appears to be the result of modifying a carnivore skull structure to the very different demands of a plant fiber diet. Davis had also studied the masticatory apparatus of the Spectacled Bear (*Tremarctos ornatus*), which shows one of the most herbivorous diets among bears (Davis 1955). The skull of *Tremarctos* is also compared with *Ursus* in a transformed coordinate grid and displays similar, though less marked, deformation trends to that of *Ailuropoda* (Davis 1964, 29). The digestive system shows only minor modifications, primarily reduced intestinal length (216-218).

In the ensuing discussion on cranial morphology, the morphogenetic mechanisms of the mammalian skull are attributed to a "mosaic of independent morphogenetic units" that become functionally integrated by selection operating on the timing of growth and differentiation, as well as external mechanical demands during ontogeny (72).[150] Support for this explanation is drawn from studies of cranial development in bulldogs and the details known about the ontogeny of the

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[150] Similar discussions are found concerning myological evolution (196-198) and arteries (274-280).

vertebrate limb. Davis is at pains to stress that the external mechanical demands during ontogeny are responsible for most of the specific skeletal morphology in the panda.

> Many of the differences between panda and bear skeletons are adaptive, but their cause is extrinsic to the bone itself; that is, they merely reflect the response of the bone tissue to external pressures, stresses, and strains, and other purely mechanical factors. In the absence of the appropriate stimulus such characters fail to appear. Among such features are the surface modeling of bones, torsions, form and extent of articular areas, and size and position of foramina. These are characteristic features of the skeleton of *Ailuropoda*, and they may be clearly adaptive in the sense of promoting the efficiency of the organism, but they are epigenetic to the bone and therefore are not the result of natural selection *on the skeleton* (122).

Natural selection did not continuously sculpt genetic differences but preserved the epigenetic results of differing mechanosensitive interactions during ontogeny (cf. Müller 2003a).

One cherished conceptual theme of embryological approaches to evolution, both past and present, is found repeatedly in Davis's explanations—morphological gradients. They appear in his discussion of the vertebral column (Davis 1964, 84-85), where 'lumbosacral peculiarities' of the panda are hypothesized to be the result of an 'accidental' (i.e. not due to selection) heterochrony, the expansion of the proximal ends of the ribs (88), and in the explanation of dentition (127-130). In the latter case, the 'field control concept' and 'differential growth' allow him to reconcile the greater similarities between giant panda and raccoon premolars with the closer phylogenetic relationship between giant pandas and bears. Davis consistently states that many changes from *Ursus* to *Ailuropoda* are not the result of numerous small mutations sculpted by natural selection but rather a few genetic changes (possibly only two mutations for skeletal differences) that were then pleiotropically magnified through ontogenetic trajectories containing distinct morphogenetic fields (122-124).

This claim did not go unnoticed. Reviewers remarked that,

> [t]he numerous morphological differences between *Ailuropoda* and bears are frankly discussed, but the evolutionary mechanisms by which Davis proposes to explain them will probably not be accepted by those who regard natural selection as the dominant force behind organic evolution. Davis insists that many anatomical features in *Ailuropoda* could not be adaptive, hence must be due to general disturbances of morphological homeostasis. He suggests that the most profound differences between giant pandas and bears resulted from the action of relatively few genes which had large, pleiotropic or even catastrophic effects (MacIntyre and Koopman 1967, 73).

Davis's claim was rejected more explicitly when his work was cited favorably in later macroevolutionary discussions, such as that of the paleontologist Steven Stanley (Stanley 1979, 55-6, 138, 157-8). Lande responded specifically to Stanley's use of Davis's work.

> Similar confusion exists concerning variation in allometric growth and developmental fields. That morphological differences between related species could be explained as simple changes in a few growth gradients or developmental fields (as attempted by Davis 1964, for the giant panda […]), does not imply that only a few genes were involved. On the contrary, evidence exists that natural variation in parameters of allometric growth and developmental fields is usually influenced by multiple genetic factors acting relatively late in development (Lande 1980, 234-5).

The use of Davis's research as contrary to neo-Darwinian tenets was also iconic in that a giant panda appeared on the cover of Stanley's book.

The pattern of explanation using morphogenesis and allometry is not unique to Davis's study of the giant panda. In his description of mammals from the lowland rainforest of North Borneo, he claims that the enlarged nose morphology of the proboscis monkey is not functionally significant and rather results from a differential growth rate in the morphogenetic mechanism of the ancestral snub nose (Davis 1962, 67). Selection need not be invoked for the unique nose of the proboscis monkey since the morphogenesis of this feature is positively correlated with body size, which exhibits a trend to increase in this lineage. The invocation of morphogenetic gradients and fields, persistent use of allometric transformations and heterochronies to explain morphological differences, a focus on evolutionary novelties such as the panda's thumb, ursid scapula, and the origin of paired limbs, consistent attention to the developmental origin of the characters under consideration, an emphasis on epigenetics and mechanical 'constraints' in ontogeny, and a desire to carefully state where natural selection is (and is not) causally responsible all situate Davis as a historical source for Evo-devo from a morphological perspective with explanations of evolutionary innovations and novelties as a central component of his research agenda.

4.6. W.K. Gregory: Paleontological Approaches to Evolutionary Innovation

4.6.1. *Evolution Emerging*: *Magnum opus*

William K. Gregory (1876-1970), protégé of Henry Fairfield Osborn, was a vertebrate paleontologist located at Columbia University and the American Museum of Natural History for most of the first half of the 20th century (Rainger 1991). At the end of his career he published a two-volume, synthetic account of evolutionary patterns and processes throughout the history of life (Gregory 1951, cited hereafter as *EE* I or II). *Evolution Emerging* is an impressive work. The first volume, which contains the textual component, runs over 700 pages (including bibliography and index). The second volume consists solely of detailed illustrations corresponding to the text, exceeds 1,000 pages, and includes numerous foldouts. It is very unlikely that a book of the same scope and presentation could ever be published today (for financial reasons), let alone attempted (because of professional specialization trends).[151] The introductory chapter begins with an overarching metaphor ("The Cosmic Cinema"), an

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[151] Carroll's *Vertebrate Paleontology and Evolution* is an approximation but more limited in scope (Carroll 1988).

articulation of his distinction between polyisomerism and anisomerism,[152] invectives against anthropomorphism, and ends with twenty-nine quatrains of poetic verse, including these two.

IV
The dolphin's equal teeth have been derived
From very unequal teeth of carnivores
Unequals changing into equal parts
Are "secondary polyisomeres"

V
But equal parts to parts unequal changed
Are, on the contrary, called "anisomeres."
As when the rows of teeth almost alike
Gave rise in crocodilians to festoons.

Various section headings and subdivisions are creatively titled (e.g. "The Sponge-State and Its Citizens" or "The Bivalves—Brainless but Successful") and the pace is breathtaking; the discussion begins with the emergence of life on Earth and moves through to human beings before reiterating and integrating larger philosophical themes (especially polyisomerism and anisomerism) in the last ten pages (*EE* I: ch. 25). Reviewers flagged Gregory's philosophical inclinations and extensive use of colorful metaphor (Jepsen 1951; Rand 1951; Straus 1954).

Who was the audience for this comprehensive discussion of the history of life, couched in unabashed personal and philosophical reflection? One reviewer claimed that Gregory's book on the process of evolution would be of interest to geneticists, paleontologists, ornithologists, taxonomists, mycologists, ecologists, morphologists, comparative psychologists, and comparative physiologists (Bates 1951). It was identified as research in systematics in an editorial in *Science* (Blackwelder 1951), whereas Jarvik cited it in regard to theories of tetrapod

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[152] *Polyisomerism* = "the state in which many homologous parts, or polyisomeres, are arranged along any primary or secondary axis, whether straight or curved." *Anisomerism* = "the state in which one or more parts are emphasized at the expense of the rest, while the original number of separate parts is usually reduced, either by fusion or by elimination" (Gregory 1934, 1; cf. Gregory 1935a). Gregory's terminology was meant to apply to purely physical as well as biological entities, which was noticed and criticized by a philosopher shortly thereafter (Plochmann 1959).

origins (Jarvik 1955). When two biologists reinvigorated the discussion of the origin of key vertebrate features (Northcutt and Gans 1983), both morphological (jaw and head) and embryological (neural crest cells and placodes), Gregory's discussion in *EE* and separate articulation of his theory of vertebrate origins (Gregory 1946) are prominently cited.

A complete discussion of *EE* is impossible herein, but my present intent is to investigate how these volumes might justifiably be understood as part of a history relevant for Evo-devo, especially as a paleontological perspective concerned with innovation and novelty. The 1983 article on vertebrate origins just cited is one obvious entry point. Another is observed in the comments of one reviewer about what is required to understand evolution.

> The synthesis, the development of understanding of the total complex of processes, will perhaps become the function of some new sort of naturalist, who can combine the gleanings of the many special sciences: of the taxonomists, morphologists and comparative physiologists who have described the present diversity of living things; of the paleontologists who have accumulated the historical documentation; of the geneticists who have dissected the mechanisms of inheritance and variation; and of the ecologists who have formulated the principles of population dynamics and analyzed the operation of environmental forces. But before this new naturalist can begin to operate, each of us must formulate, synthesize and clarify the content of his special science, keeping in mind the needs and perspectives of this new, emerging field. This Dr. Gregory has done, providing us with a work that each of us can use in his special field, and that all of us can use in building toward this broader understanding of the living universe (Bates 1951, 394).

That *EE* could serve as a stimulus toward a synthesis of biological disciplines with respect to explaining evolutionary history exhibits a theme that resonates with Evo-devo as a multidisciplinary synthesis (cf. Section 1.1 and Section 4.2). In what follows, I restrict my attention to portions of Gregory's text that juxtapose evolutionary and developmental themes with particular emphasis on innovations and novelties.

4.6.2. *Evolution Emerging*: Evolution and Development

Gregory's welding of evolution and development displays continuity with earlier research in that Haeckelian themes linger throughout, which can be observed in his specific explanations for the origin of novel biological features.

> In the coelenterates (hollow intestine), including the highly varied hydroids, jellyfishes (medusae), corals, seafans, etc., the body is essentially cup-like, derived from the outer and inner layers of the gastrula stage of the embryo. This cup-like condition of the gastrula stage is due to the faster growth of the smaller ectoderm cells, which grow around and enclose the larger, nutriment-bearing endoderm cells. Thus the adult coelenterates may be regarded as forms which have never gone far beyond the gastrula stage (*EE* I: 26).

Other examples abound, such as the comment that horseshoe crabs literally go 'through' a 'trilobite larval stage' (*EE* I: 61) or the observation that ontogeny mirrors phylogeny in brachiopod valve development (*EE* I: 77). These recapitulatory themes bear on his understanding of the origin of innovations and novelties because "advanced larval forms often become the starting-point for new lines of evolution", as well as the origin of new taxa, such as spiders from scorpions via 'paedogenesis' (*EE* I: 63), or trigger fishes through 'metamorphosis or transformation' (*EE* I: 196-7). By 'paedogenesis' and 'metamorphosis or transformation', Gregory has in mind a recapitulatory notion of heterochrony understood primarily in terms of "acceleration and retardation of growth" (*EE* I: 38).[153] Another example is his explanation of the origin of scorpion fishes:

> However, it is not necessary to push the scorpaneid stem back to the berycoid stock, because the stages in the development of the rosefish …indicate that all we need to assume is that there was a great increase in the size of the eye and an accelerated individual development of it, so that at a relatively early stage it became the dominant organ, around which the preopercular and suborbital Anlagen formed a continuous tract.

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[153] "According to this principle, certain ancient embryonic features which are ordinary [*sic*] passed through before the adult stage are sometimes retained in the adult by the lagging of later growth stages wither in vigor or in timing" (*EE* I: 363).

> …The subsequent downward growth of the hyomandibular and preopercular, together with the forward growth of the jaws, plus the necessary growth force of the suborbital itself, all coöperated to produce the observed result (*EE* I: 209).

These types of explanation are common and strewn throughout Gregory's discussions of different taxa and their attendant evolutionary innovations and novelties, including 'The Role of Paedogenesis in the Ancestry of Modern Urodeles" (*EE* I: 253).

Recapitulatory themes are pictorially represented in Gregory's illustration of the origin of the vertebrates, 'From Animated Seed-Capsule to Motile Adult by Neoteny" (*EE* II: 84; Figure 5).

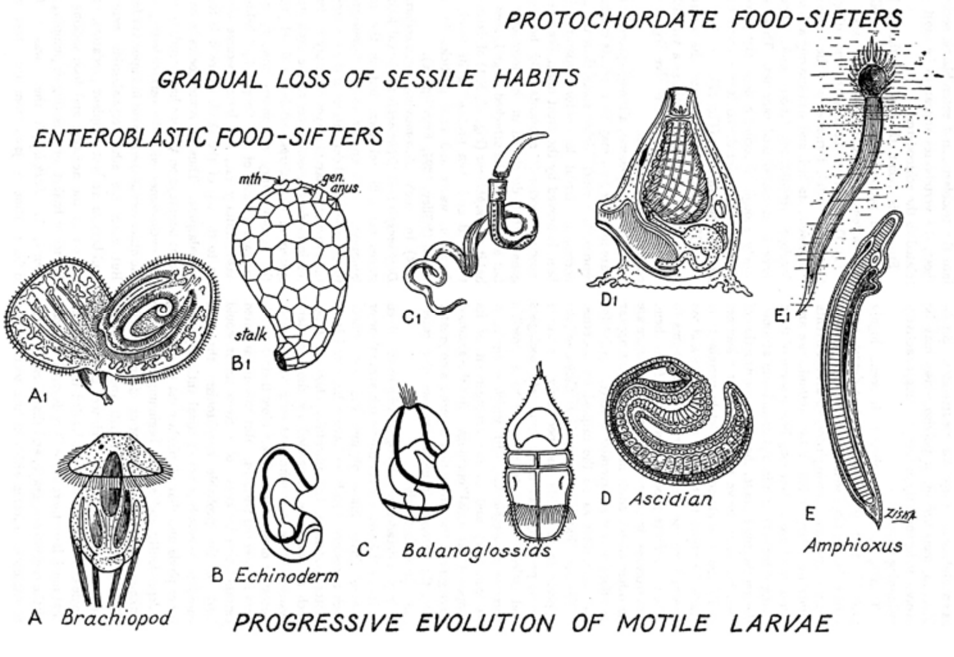

Figure 5: Gregory's Conception of the Origin of Vertebrates

Courtesy of American Museum of Natural History

His discussion of the Devonian palaeoniscoid *Cheirolepis* is a good narrative exemplar of how developmental data are enlisted to understand the origin of evolutionary novelties through an extension of a developmental trajectory.

> [T]he bilateral symmetry of his body was doubtless due to the symmetrical budding of metameric segments on either side of the blastopore, with resulting pushing of the older buds toward the rear …This also permitted the differentiation of the head-end from the tail. The longer the period of growth and multiplication of the proto-vertebrae, the greater was the number of vertebral segments and the approach toward an eel-like larval stage. Thus a simple prolongation of certain stage of growth may in the course of time induce striking changes in body form (*EE* I: 229).

Paedogenetic events can also explain problematic characters, such as 'reptilian' features in monotremes (*EE* I: 363-6), bringing resolution to phylogenetic confusion. All of these examples are a reminder that many of Gregory's concerns are derived from debates about phylogeny among comparative anatomists from 1880-1930, especially vertebrate origins (Bowler 1996; Gregory 1946). Lacking fossil record evidence, data from embryology and comparative anatomy were the only route to phylogenetic hypotheses (*EE* I: 51).

Yet Gregory's concerns were not wholly phylogenetic. In an article published in the journal *Evolution* a few years after *EE* (Orton 1955), Gregory's 1946 work (repeated in *EE*) is explicitly noted for discussing the relation between development and evolution, especially his theory that defining, novel characteristics of chordates and vertebrates (e.g. notochord and somites) could have arisen as larval specializations that were locked in via neoteny.[154] Developmentally oriented explanations of innovations and novelties abound in *EE*. In his discussion of coelenterates, Gregory poses the question of how the efficient, poisonous 'dart-cell mechanism' arose. He takes it as a requirement for *any* explanation that it consider the developmental fact that the cnidoblast ('stinging cell'), which houses the components responsible for the mechanism ('nematocysts'), does not originate in the tentacle but rather migrates from elsewhere to its eventual epidermal location. His tentative explanation includes a discussion of nematocyst cell lineage (*EE* I: 26-7). Spirality in gastropods is not just articulated with respect

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[154] Gregory's hypotheses are cited alongside those of de Beer's in this same article (de Beer 1951; cf. Hall 2000).

to shell shape or color patterns but also the twist of the visceral nerve loop that occurs during ontogeny (*EE* I: 41). The origin of insect wings (*EE* I: 66), the notochord (*EE* I: 88), bone (*EE* I: 106), the oralo-branchial cavity in cephalaspid ostracoderms (*EE* I: 107), the shift to a cartilaginous head and body in lampreys (*EE* I: 108), the origin of electric organs (*EE* I: 137-8), the Weberian apparatus in the fish order Ostariophysi (e.g. carp or catfish; *EE* I: 160-1), color patterns in teleost fishes (*EE* I: 184-191), the origin of the oddly placed 'sucking disc' from the dorsal fin in sucking fishes (*EE* I: 206-7), the fan-like dental plates in lungfishes (*EE* I: 237-8), distal skeletal elements of the tetrapod limb (*EE* I: 246), the origin of frogs by modification of the vertebrae and ribs during larval stages (*EE* I: 252-3), the emergence of feathers (*EE* I: 314-5), the origin of the diaphragm (*EE* I: 334-5), mammalian hair, skin, and ears (*EE* I: 344-7), the transition from platypus bill to echidna snout (*EE* I: 365), the transition from cynodont reptile skull to opossum skull (*EE* I: 366-7), the presence of extra zygapophysial processes in the vertebrae of Xenarthan edentates (e.g. armadillos; *EE* I: 390), and the cranial shape of orangutans (*EE* I: 480) are all explored through developmental considerations.[155] There are also several discussions of mechanical forces potentially shaping morphology during ontogeny, such as in the crests and ridges of sauropod vertebrae (*EE* I: 301-2, 304).

In addition to the case of gastropod ontogeny (*EE* II: 13), it is also worthwhile to note the frequent developmental representations utilized by Gregory. Despite the fact that the primary illustrations throughout are either phylogenetic, morphological, or paleontological, there are also pictorial representations for the ontogeny of brachiopods (*EE* II: 60), echinoderms and balanoglossids (*EE* II: 65), *Nereis* and *Amphioxus* (*EE* II: 69), ascidians (*EE* II: 70), silver sharks (*EE* II: 123), the rosefish (*EE* II: 297), turtles (focused on the carapace; *EE* II: 397), the vertebrate inner ear (*EE* II: 597, 610, 613), and marsupials and the platypus (*EE* II: 654). This

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[155] Many of these explanations were contentious and criticized by reviewers (Rand 1951, 437-8).

reveals a significant theoretical slant to how evolutionary relationships are to be discerned and character transitions explained. This does not even touch upon the in-text descriptions of development that repeatedly occur in volume 1 (e.g., *EE* I: 79ff).

Gregory attempted to draw out general (though arguably cryptic) principles relevant to thinking about the origin of innovations and novelties from these specific examples.

> When a new hereditary structural feature becomes widely distributed in a large population, its further progress or decline may be due to generally uniform or recurrent preëxistent forces or conditions; in other words, it may follow certain precedents, general patterns, rules or laws observable in many similar cases. But the same new characteristic or organ, in so far as it is new, arises not from any one of the various forces or conditions that were prerequisite for its existence but from the new and repeated intersections of all these prerequisite series of forces and conditions at particular moments of time and locations in space. It is the concurrence of such unpredictable intersections of various forces and conditions at given moments that give rise to what is called chance or luck, which has operated in the world of animals with chitinous articulated skeletons much as it has in the world of articulately speaking men (*EE* I: 61).

Gregory is driving at a general notion of 'evolutionary chance' that will give unique, historical explanations for the origin of new structures and functions while incorporating preexisting constraints and general rules or patterns. In his review comments on 'from ganoids to recent teleosts', he rules out Lamarckism as a possibility and utilizes embryology to explain dorsal-ventral differentiation and streamlining (*EE* I: 226-7). This discussion also contains a statement that the 'polyisomeres' that are 'anisomerized' through adaptive specialization arise or originate from 'centers of organization' or 'fields of force' during ontogeny (*EE* I: 228, 553). The emergence of new polyisomeres is attributed to processes of 'budding' during ontogeny and "is the rule in many cases of increase in the number of vertebral segments, of teeth, fin-rods, etc" (*EE* I: 246). The 'lock and key' fit between accessory reproductive organs in opposite sexes, the interlocking relations among carpal bones in mammals, and the occlusal relations between upper and lower teeth is largely due to the ontogenetic *and* phylogenetic "buckling up, folding, invagination, evagination, etc., of an originally extended tissue layer or layers" (*EE* I: 510).

One would be remiss not to take into account other aspects of Gregory's work besides *EE*. An interesting convergence between Davis and Gregory is found in their predilection for *functional* morphology (Rainger 1991, ch. 9).[156] In this respect these two individuals are not easily categorized as idealist leaning morphologists and paleontologists trapped in typological thinking. Gregory's employment of recapitulation was not naïve.

> Since Patten's time the dogma of recapitulation has been pretty well deflated by T.H. Morgan and others. But with reference especially to the lower invertebrates (e.g. Coelenterata, Annulata, Echinodermata, Brachiopda [*sic*] and others) it is still probable that larval or young stages may often but not always retain some earlier phylogenetic features which are lost in the adults (Gregory 1950, 170).

He utilizes the principle 'tentatively', always being careful to highlight the methodology before proceeding (e.g. *EE* I: 77-8), and recognizes alternate uses. "The embryonic development of a given *organ* or *group of organs* may or may not give reliable indications of the remote history of the animal; yet it may also give fairly indirect evidence as to the relationships of the animal to other systematic groups having similar embryonic stages or processes" (*EE*, I: 85 [my emphasis]; cf. Gould 1977, 170-5). In some cases the embryological evidence is patently misleading, as in the inner skull of vertebrates (*EE* I: 260-1), and is therefore only utilized in conjunction with a broad array of other skeletal features to infer phylogeny.

Though some of Gregory's penchant for recapitulatory explanations (either of evolutionary transitions or phylogenetic relationships) is attributable to the milieu of his training in paleontology at the outset of the 20th century, his reflective utilization of these ideas over fifty years later through multiple examples directs us to see more. The link between morphology,

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[156] Rainger highlights the fact that Gregory's research program was just as much morphological as it was paleontological (Rainger 1991, 220-224).

paleontology, development, and the concepts of EVOLUTIONARY INNOVATION and NOVELTY is persistent and inescapable, compelling us to recognize figures like Gregory, and paleontological research more generally, in any historical picture of Evo-devo (cf. Hall 2002).

4.7. Synthesis

What benefits are derived from identifying Davis, Gregory, and Berrill as historical sources pertaining to Evo-devo via the concepts of EVOLUTIONARY INNOVATION and NOVELTY? There are at least three possibilities. First, developmental genetics has received tremendous historical attention because it is a central part of contemporary Evo-devo and these histories converge with the genetics and (experimental) embryology exclusion perspective. Although some advocates sensitive to the paleontological aspects of Evo-devo have cited *Evolution Emerging* (Hall 1999a; Raff 1996),[157] Davis is not discussed and many articles in the survey are ignored, even when they seem obviously relevant. Berrill is recognized by those who continue to work on tunicates from an Evo-devo perspective (Jeffery and Swalla 1992), but his larger influence on the problem agenda inherited by modern Evo-devo is not well recognized (Love and Raff 2003; Raff and Love 2004). Painting a more complete picture of various historical trajectories relevant to contemporary Evo-devo is a beneficial outcome of attending to these perspectives through the problem agenda of innovation and novelty as a historiographic principle of choice.[158]

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[157] Neither author explores Gregory's work in detail. Hall makes the connection between paleontology and Evo-devo very explicit in a recent review, although Gregory's contribution is not discussed (Hall 2002).

[158] Analytical techniques such as morphometrics within Evo-devo (Roth and Mercer 2000) also emphasize the connection between morphometrics and ontogeny in morphological research (Olson and Miller 1999 [1958], ch. 7).

Second, it is significant that none of these researchers was hostile to the Modern Synthesis.[159] Davis was a formal participant (Davis 1949a), Gregory made numerous favorable remarks about the results of genetic research on evolutionary mechanisms (especially natural selection) in the work of individuals such as Wright or Dobzhansky (*EE*, I: 280-1, 454, 510, 513, 536, 557, 559), and Berrill's main axe to grind concerned the molecularization of developmental studies. This point can be emphasized through the irony that one reviewer of Gregory's *EE* held that "if there is any weak point, it is in the high degree of efficacy attributed to natural selection" (Rand 1951, 438). This criticism was made with respect to the origin of a particular innovation, the electric organ of fishes.[160] At the same time, Davis was accused of being anti-selectionist in his explanations (e.g. in reviews of his giant panda monograph) and in connection with its co-option by Steven Stanley for his book *Macroevolution*. But Davis's ire was actually directed at the seemingly hegemonic discipline of genetics, which had grown significantly through the 1950s, rather than the Modern Synthesis. On the reverse of the title page to the giant panda monograph he quoted Goldschmidt approvingly: "The field of macrotaxonomy … is not directly accessible to the geneticist… Here the paleontologist, the comparative anatomist, and the embryologist are supreme."[161] The real concern lies in the recognition of different levels of organization in biological entities, something that is forcefully expressed in Berrill's articulation of the need to ask questions at higher levels of organization in ontogeny to understand the emergence of evolutionary novelties.

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[159] Open hostility is not difficult to isolate in others. "There are certain facts which, although they may have been stated before, have not been adequately understood, particularly by geneticists. …The Neo-Darwinians may find explanations for them; if so very well; but if not these facts should not simply be ignored, and if a theory of another kind can explain them better, it should be given consideration" (Brough 1958, 17).

[160] "The transformation of muscle to electric tissue requires radical histologic and functional changes in the muscle. To assume sufficiently numerous successive mutations in the same direction is hardly justifiable" (Rand 1951, 438).

[161] This comment also blends the origin of higher taxa (*taxonomy*) with origin of novelties (*macro*evolution).

Finally, recognizing the significance of different levels of biological organization redirects our attention to evaluating what morphology, paleontology, and comparative embryology can contribute to evolutionary theory today. Arguably, higher levels of structural organization were neglected in the Modern Synthesis, which gave us a ‘two-level’ theoretical structure of genotype and phenotype. Paying attention to this feature may be critical for the future unfolding of Evo-devo as a research discipline. Since most of the innovations and novelties that exercise researchers tend to occur at high levels of organization, the necessary role of morphological research within Evo-devo *qua* disciplinary synthesis is made clearer. Morphologists, paleontologists, and comparative embryologists provide the analysis of evolutionary novelties at these higher levels of organization while developmental biologists (‘experimental embryology’) account for the generative principles of their construction from lower levels of organization during ontogeny, mostly in the form of gene expression and function studies. This also allows a rational reconstruction of the ‘exclusion of embryology’ in the Modern Synthesis in terms of an inordinate focus on lower levels of organization in terms of population genetics (evolution as changes in allele frequencies). Researchers who worked on elucidating processes in a developing organism responsible for constructing higher levels of organization were sidelined. This is a very different interpretation of what occurred in the Modern Synthesis. Now that proponents of Evo-devo are renegotiating the relations between evolutionary and developmental biology, these historical perspectives may provide useful material for navigating ongoing research on evolutionary innovations and novelties.

4.8. Remainders and Summary Remarks

In conclusion it is necessary to acknowledge that my historical presentation is biased in its textual/exegetical orientation rather than adopting a narrative of various contextual elements that foreground social factors pertinent to these individuals and their institutional homes. For example, one could draw attention to the differences between the University of Chicago/Field Museum of Natural History for Davis and Columbia University/American Museum of Natural History for Gregory or even Berrill's home at McGill University in Canada. Addressing the work of other researchers in this time period is also required to strengthen the conclusions I have drawn here. Returning to the systematics analogy used in developing the phylogenetic approach to philosophy of science, more taxonomic sampling is required. Further neglected components in my analysis include the culture and material practices of these biologists (cf. Pickering 1992).

There are also interesting connections between particular explanations offered by these researchers. Davis's effort to demonstrate that the giant panda was a modified bear was in part directed at Gregory's view that the giant panda was more closely related to lesser pandas and raccoons. i.e. procyonids (Gregory 1936). A key character in the dispute was dentition and we have already observed that Davis appealed to morphogenetic fields in dental development to bolster his own case. The taxonomic question is not idle for understanding the role of Davis's invocation of development in the context of alternate explanations of evolutionary change. Two reviewers captured this explicitly:

> If *Ailuropoda* were to be regarded as a kind of lesser panda which had relatively recently made an adaptive shift into a new niche (involving selection for larger size and more powerful jaws and teeth), then many of the apparently non-adaptive features particularly in the locomotor complex, might be explicable on a selectionist basis (MacIntyre and Koopman 1967, 73).

More recent phylogenetic studies utilizing molecular characters vindicate Davis's conclusion (Goldman, Giri and O'Brien 1989; O'Brien 1987; O'Brien *et al.* 1985; Sarich 1973; Zhang and Ryder 1993), although whether this constitutes a 'solution' to an outstanding controversy or reaffirmation of Davis's own careful anatomical work is debated.[162] The lesser (red) panda remains a taxonomic anomaly within the order Carnivora (Flynn and Nedbal 1998; Flynn *et al.* 2000; Flynn, Neff and Tedford 1988). Berrill also clashed with Gregory regarding vertebrate origins, the former having the 'ascidian' focused explanatory account (Section 4.4) in contrast to Gregory who favored a secondary derivation of ascidians (and amphioxus) from a basal chordate or even ostracoderms (Gregory 1946). Recent work supports neither researcher (Holland and Holland 2001; Holland and Chen 2001), although (again) it is difficult to say whether genuine consensus has been reached.

We began in Section 4.2 with the identification of a bias in the historiographic premises used to explore history relevant for Evo-devo. These genetics and embryology exclusion histories do not capture key features of the emergence of contemporary Evo-devo. They concentrate on the history of experimental embryology that bequeathed the molecular developmental genetic tools currently available while ignoring the evolutionary developmental problems that researchers are and have been focused upon. Using the problem agenda of innovation and novelty as a historiographic guide for choosing sources allows us to recover overlooked historical material. In Section 4.3 we captured the basic outline of studies of evolutionary innovation and novelty, identifying predominant disciplinary foci (comparative embryology, morphology, and paleontology), a bias towards analyses of structure over function, and differences in descriptive language for the subject matter ('origin of higher taxonomic categories').

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[162] See the correspondence between Flynn, Wyss, and O'Brien in *Scientific American*, June 1988.

The next three sections treated exemplars from each of the disciplinary foci and their explanations of evolutionary innovation and novelty in much more detail: N.J. Berrill, D. Dwight Davis, and W.K. Gregory. Section 4.7 synthesized these case studies, showing how they are valuable additions to a history of Evo-devo's research problems that are not yet fully appreciated. The main issue for these individuals was not the Modern Synthesis *per se* but rather the lack of attention to higher levels of structural organization that were the province of comparative embryologists, morphologists, and paleontologists. This provides a different conceptualization of what the Modern Synthesis did or did not exclude and why certain kinds of researchers may have been more or less inclined towards its theoretical orientation.

5. CONTEMPORARY EXPLANATIONS OF INNOVATION AND NOVELTY

5.1. Introduction

Explaining the origin of novel features in the history of life constitutes an enduring problem agenda in evolutionary research (Müller and Wagner 2003). It was sidelined in (though not absent from) the middle part of the 20th century when population genetic approaches to evolutionary investigation and definitions of evolutionary change in terms of allelic frequencies gained ascendancy. Questions regarding how variation relevant to innovations and novelties originated developmentally were subordinated to explanations in terms of selection operating on alleles in Mendelian populations subject to migration, mutation, and recombination (Mayr 1960). This was in marked contrast to disciplinary studies at higher levels of organization (comparative embryology, morphology, and paleontology) that perceived an understanding of development as a prerequisite for explaining innovations and novelties. The 'return of the embryo' to evolutionary research in Evo-devo has rejuvenated attempts to explain novelties through a mechanistic understanding of ontogeny (Love 2003a, in press; Raff 1996; Wagner 2000; Wagner, Chiu and Laubichler 2000; cf. Chapter 1). Much of Evo-devo can be understood as tackling old problems from the domain of comparative evolutionary embryology with new molecular biological tools from the heritage of experimental embryology (Love and Raff 2003; Raff and Love 2004).

One of the distinctive aspects of current Evo-devo methodology is the toolkit of developmental genetics, which has been the primary route to empirical data concerning innovations and novelties over the past decade (Carroll, Grenier and Weatherbee 2001; Marshall, Orr and Patel 1999).[163] A recent National Human Genome Institute Research working group identified innovations as a condition on the selection of new genomes for sequencing: "the provision of sequence from critical phylogenetic positions, for example to illuminate the evolution of major morphogenetic or physiological innovations in evolution" (http://www.genome.gov/11509736). This methodological preference sometimes translates into a claim about the causal factors most relevant for explaining the origin of novelties.

> The evolution of new morphological features is due predominantly to modifications of spatial patterns of gene expression (Gompel *et al.* 2005, 481).
>
> Evolutionary change in the form of body parts requires evolutionary change in the gene regulatory network that controls pattern formation processes … For anyone interested in mechanism, there is in fact no other way to conceive of the basis of evolutionary change in bilaterian form than by change in the underlying developmental gene regulatory networks (Davidson, E. H. 2001, 157, 201).
>
> Evolution and development are both manifestations of the heritable genomic regulatory programs that determine how the morphological characters of each species are built. … A syllogism leads to the evolutionary process by which morphological characters arise and diversify: the body plan of each taxon at each developmental stage consists of conserved plus novel morphological characters (with respect to phylogenetic relatives), and morphological characters depend causally on the operations of developmental [gene regulatory networks]; therefore, evolutionary conservation and novelty in form must devolve from retained and novel features of [gene regulatory network] architecture (Hinman *et al.* 2003, 13356).[164]

Some researchers have proposed that any principles concerning the origin of novelties that obtain at the genic level are also applicable to other levels of organization (Ganfornina and Sánchez

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[163] Phylogenetic systematics (cladistics) is also critical in current Evo-devo (Telford and Budd 2003).

[164] Although these claims concern evolutionary novelties, one can also observe similar causal claims about development (cf. Love forthcoming; Robert 2004). "During evolution, it is the change in genes that leads to the creation of new patterns of development" (Wolpert and Szathmáry 2002, 745); "Complex developmental change is intrinsically based on sequences of key genetic activities" (Wilkins 2002, 505).

1999). These methodological preferences motivate the genetics and embryology exclusion histories detailed in Chapter 4 (cf. Wilkins 2002, ch. 4). The putative equivalence of molecular developmental genetics and Evo-devo is not subtle.[165]

Molecular developmental genetic approaches, while powerful, should be carefully appropriated in investigating innovations and novelties because many of these features are complex organismal structures or functions at higher levels of organization that require a multitude of interacting genes and morphogenetic processes throughout ontogeny for their construction. Old *morphological* problems are being approached with new *molecular genetic* tools. The significance of this disparity in the levels of organization under scrutiny, which we captured in part with the molecular paradox, will be fully addressed in Chapter 6 when we compare contemporary explanations of innovation and novelty with the criteria of explanatory adequacy detailed for the problem agenda. This chapter is devoted to understanding the structure of contemporary explanations of evolutionary innovations and novelties, especially those utilizing developmental genetics.

Section 5.2 surveys developmental genetic explanations of evolutionary novelty, focusing on the now famous *Hox* genes (in arthropods), and sketches a preliminary analysis of their structure. Section 5.3 is an extended case study, the origin of vertebrate jaws, emphasizing recent research from a developmental genetic perspective.[166] A shorter case study is covered in Section 5.4 on larval evolution in sea urchins to illuminate the operational determination of non-homology in the absence of fossil forms. Section 5.5 details other disciplinary approaches to innovation and novelty found in contemporary biology. These alternate explanatory strategies

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[165] "The discovery of the homeobox in 1984 and, immediately after, the discovery of Hox genes in a variety of organisms, including mammals, opened the road for comparative molecular genetics, now simply called evo/devo" (Deutsch 2001, 757).

[166] Recall that details regarding developmental genetic explanations of avian feather origination are in chapter 3.

provide a contrast to developmental genetic explanations of innovation and novelty. I end the chapter with a brief distillation of salient themes among these contemporary attempts to explain innovation and novelty and identify differences in disciplinary approaches relevant to the disciplinary synthesis of Evo-devo.

5.2. Developmental Genetic Explanations of Innovation and Novelty

5.2.1. Brief (Arthropod) Survey

Evo-devo research on the origin of arthropod morphological features provides a window to survey the style of developmental genetic explanations of evolutionary innovation and novelty. Many of these have focused on the role of *Hox* genes (McGinnis 1994; McGinnis and Krumlauf 1992), especially in segment identity and morphology (Carroll 1995; Carroll, Grenier and Weatherbee 2001; Hughes and Kaufman 2002; Nagy 1998). *Sex combs reduced* (*Scr*) has been linked to the suppression of wing formation and promotion of leg combs in insects, allowing for the origin of specializations in the prothorax (Rogers, Peterson and Kaufman 1997). *Deformed*, *proboscipedia*, and *Scr* execute novel roles in the specialized sucking mouthparts of hemipterans (Hughes and Kaufman 2000), the drosophilid proboscis (Abzhanov, Holtzman and Kaufman 2001), and crustacean head morphology (Abzhanov and Kaufman 1999a). Duplication of the *engrailed* gene in higher crustacean lineages is associated with novel expression domains related to head segment morphology (Abzhanov and Kaufman 2000c). Other changes in *Hox* expression are involved in the origin of body segment features, such as the first thoracic leg into mouthpart maxillipeds (Abzhanov and Kaufman 1999b, 2000b; Averof and Patel 1997), and various transformations of trunk and limb morphology between insects and crustaceans (Abzhanov and Kaufman 2000a; Brena *et al.* 2005; Hayashi, Yamagata and Shiga 2003).

Ultrabithorax represses limb formation in insects (in contrast to crustaceans) via a modification of a C-terminal serine/threonine phosphorylation site (Galant and Carroll 2002; Ronshaugen, McGinnis and McGinnis 2002; cf. Weatherbee and Carroll 1999).

The origin of pigment patterns in *Drosophila* species results from changes in the regulation of the *yellow* gene (Gompel *et al.* 2005) and the origin of sexual dimorphic coloration involves regulatory changes controlling the *bric-a-brac* gene (Kopp, Duncan and Carroll 2000; cf. Gompel and Carroll 2003). In butterflies, eyespot origin and evolution has been thoroughly explored (Beldade and Brakefield 2002; Beldade, Koops and Brakefield 2002a, 2002b; Brakefield and French 1999; Brakefield, French and Zwaan 2003; Nijhout 1991, 1994, 2001), with key roles identified for *distal-less*, *engrailed*, *hedgehog*, and *spalt* (Beldade, Brakefield and Long 2002; Brakefield, French and Zwaan 2003; Brunetti *et al.* 2001; Keys *et al.* 1999). Another domain of interest is the origin of segmentation, motivated in part by cross-phylum interest in annelid and chordate segmentation (Carroll 1995; Damen, Weller and Tautz 2000; Davis and Patel 1999; Schoppmeier and Damen 2005; Seaver 2003; Stollewerk, Schoppmeier and Damen 2003; Wilkins 2002, ch. 7). The downstream activation of apoptotic genes via *Deformed* 'sculpts' the head segment via cell death in *Drosophila* (Lohmann *et al.* 2002). *Hox* gene expression patterns have also been marshaled to solve conundrums concerning the homology of body segments between chelicerates and other arthropods (Abzhanov, Popadic and Kaufman 1999; Damen *et al.* 1998; Telford and Thomas 1998).

Despite this arthropod bias, molecular developmental genetic investigative strategies using regulatory genes are being applied to a wide variety of invertebrate and vertebrate novelties (innovations have received less attention). Examples include the turtle carapace (Burke 1989, 1991; Gilbert *et al.* 2001; Kuraku, Usuda and Kuratani 2005; Lee 1997; Loredo *et al.*

2001; Rieppel 2001; Rieppel and Reisz 1999), the origin of eyes (Arendt 2003; Arendt *et al.* 2004; Arendt and Wittbrodt 2001; Gehring and Ikeo 1999; Kozmik *et al.* 2003; Pichaud and Desplan 2002), the chordate nervous system (Ghysen 2003; Holland 2003; Lowe *et al.* 2003; Poustka *et al.* 2004), appendages, including the tetrapod limb and digits (Ahn and Joyner 2004; Capdevila and Belmonte 2000; Chen *et al.* 2005; Dudley, Ros and Tabin 2002; Metscher *et al.* 2005; Minelli 2003b; Nelson *et al.* 1996; Neyt *et al.* 2000; Panganiban *et al.* 1997; Shubin, Tabin and Carroll 1997; Sordino, van der Hoeven and Duboule 1995; Sun, Mariani and Martin 2002; Tabin, Carroll and Panganiban 1999; Tanaka *et al.* 2002; Wagner and Chiu 2001; Weatherbee and Carroll 1999), and cephalopod prehensile arms (Lee *et al.* 2003). Several related studies focus on the *loss* of a particular morphological feature such as pelvic reduction and limb loss (Bejder and Hall 2002; Cohn and Tickle 1999; Lande 1978; Shapiro *et al.* 2004) or cavefish eyes (Jeffery and Martasian 1998; Yamamoto *et al.* 2003; Yamamoto, Stock and Jeffery 2004).

5.2.2. Structure

Developmental genetic explanations of the origin of novelties have a specific (though not always explicit) structure. The core aspect of this structure is a two-step investigative procedure. The first step concerns evolutionary *pattern*, the assessment of relevant homologies and lack thereof. The second step concerns evolutionary *process*; ascertaining the origin of variation that could lead to the transformation of ancestral features to a derived novel character at the particular phylogenetic juncture while remaining within an ecologically plausible selection context (i.e. selection is a background condition). These are sequentially related, as judgments of homology are a prerequisite for postulating any particular morphological transition.

5.2.2.1. Pattern

Since developmental genetics focuses on gene expression and function, evolutionary patterns at phenotypic levels of organization are sometimes postulated using correlative similarities in the spatial and temporal expression patterns of particular genes. Some examples of attempts to establish homologies across distinct body plans by use of regulatory gene expression patterns include segmentation between arthropods and chordates (Seaver 2003; Stollewerk, Schoppmeier and Damen 2003), dorsal-ventral axis inversion and foregut homology between protostomes and deuterostomes (Arendt, Technau and Wittbrodt 2001; De Robertis and Sasai 1996; Gerhart 2000; Nederbragt, van Loon and Dictus 2002), bilateral symmetry across metazoans (Finnerty 2003; Finnerty *et al.* 2004), eye photoreceptor types among metazoa (Arendt 2003; Arendt and Wittbrodt 2001), and homologies of nerve cords and cell populations among chordate groups (Holland and Holland 2001; Holland, Holland and Holland 1996; Holland and Chen 2001; Holland and Holland 1999).

Many of these Evo-devo studies of homology utilizing gene expression patterns have been criticized. One criticism is the disparity between the hierarchical level of the feature being assessed for homology (complex morphology) and the level from which evidence is elucidated (molecular genetic expression) (Abouheif 1997; Abouheif *et al.* 1997; Bolker and Raff 1996; Dickinson 1995). This disparity is significant because gene expression can be co-opted or result from convergence (Lowe, Issel-Tarver and Wray 2002; Lowe and Wray 1997; Raff 1996; Sucena *et al.* 2003; True and Carroll 2002; Wray and Lowe 2000), homologous genes can become dissociated from homologous features (Abouheif *et al.* 1997; Wray 1999a), and ontogenetic trajectories can become rearranged to produce structural homologues at higher levels of organization that arise from different developmental processes (Roth 1988; Shubin 1994; Wagner 1989a; Wagner and Misof 1993). The ability for the independent evolution of different levels of organization, especially genotype and phenotype, has been referred to as ‘phenogenetic drift’ or ‘developmental systems drift’ (True and Haag 2001; Weiss and Fullerton 2000). Inferences of homology at significant phylogenetic distances become more suspect (Wagner and Misof 1993; Wray 1999a; Wray and Lowe 2000).[167]

Another criticism is that the confidence in making judgments in such widely separated taxa is *functional*; i.e., there is an expectation that the developmental regulatory genes will be accomplishing a similar developmental role. While similar DNA sequences do have similar molecular functions, and thus a homeodomain containing protein can be expected to bind DNA in phylogenetically distant species, the developmental role invoked for homology is not this molecular function but rather the contribution to some developmental phenotype such as axial patterning (Manak and Scott 1994). This is a violation of the longstanding dictum that homology is about the identity of structure regardless of function (Owen 1843). (The genes themselves are deemed orthologous by virtue of their structural similarity with respect to nucleotide sequence.) The basis for treating the developmental role (function) as homologous is the retention of complexity in the interactions among regulatory genes, sometimes referred to the ‘complexity criterion’ of homology (Telford and Budd 2003; cf. Finnerty 2003). These shared developmental genetic pathways and their primary consequences (axes, cell types, or tissue specification) purportedly reflect inheritance from a common ancestor. Even though this criterion is intuitive, most of these genes are multi-functional signaling molecules or transcription factors. Their function is as multi-use ‘switches’, initiating cascades that lead to transcriptional regulation and subsequently fate specification and commitment. Therefore, these genes are *likely* to be subject to convergent recruitment in the construction of similar phenotypic outcomes that require

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[167] This empirical research was invoked when discussing the molecular paradox in chapter 2. The molecular paradox also affects the pattern component of explanations of evolutionary innovations and novelties.

developmental genetic pathways early in development (i.e. parallelism), as empirical research now amply indicates.

These pitfalls can largely be avoided by making comparisons in closely related species, where co-option and dissociation are less likely and homoplasy is less of a confounding variable. But some researchers have shied away from this strategy because developmental regulatory gene expression shows *too much* conservation at short taxonomic distances and thus appears uninformative. Although this is not universally true (Moczek and Nagy 2005; Wilson, Andrews and Raff submitted), looking at structural genes offers another potential solution (Parichy 2001; Section 5.4). Because structural genes tend to be expressed in greater amounts, being the downstream targets within embryonic territories and modules undergoing differentiation and fate specification, the process of assessing gene expression patterns is practically simpler. Sequence conservation in the coding region can be expected for short taxonomic distances and alterations in expression patterns are likely to be informative.

5.2.2.2. Process

In contrast to judgments of evolutionary pattern, evolutionary process explanations require accounts of *differences*, so developmental genetic explanations must put forward empirical evidence of differing gene expression patterns and functional roles relevant to a phenotypic outcome in two phylogenetically relevant species for the novelty under scrutiny.[168] Although in principle any gene can be studied in this manner, the majority of effort is expended on regulatory genes (transcription factors, growth factors, signaling molecules) rather than structural genes, as was also observed for homology judgments.

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[168] Phylogenetic relevance was discussed in Section 2.3.2.3 and will be revisited in Section 6.4.2.3.

These differing gene expression patterns can be linked together in an evolutionary narrative of phenotypic change with a particular rationale for the molecular change. The most frequently discussed is the evolution of upstream *cis*-regulatory elements involved in gene regulation through the binding of transcription factors (Arnone and Davidson 1997; Cameron, Peterson and Davidson 1998; Carroll, Grenier and Weatherbee 2001; Davidson, E. H. 2001; Harbison *et al.* 2004; Levine and Tijan 2003; Ohta 2003; Stern 2000; Tautz 2000; Wilkins 2002, ch. 9; Wittkopp, Haerum and Clark 2004; Wray 2003; Zuckerkandl 2001). Most genes have a region upstream of their 5' promoter with different modular elements where proteins can bind to either initiate or prevent transcription.[169] A combination of different molecules leads to transcriptional activation or repression at particular places or times during embryogenesis. For example, the sea urchin endoderm gene *Endo16* has six functional elements that bind thirteen different proteins at high specificity; one element drives expression in late embryo midgut whereas another represses expression in adjacent ectoderm (Davidson, E. H. 2001, 54-62; Yuh, Bolouri and Davidson 2001; Yuh and Davidson 1996). For the vertebrate *Hoxc8* gene, specific differences in enhancer elements are directly related to differences in axial morphology (Anand *et al.* 2003; Belting, Shashikant and Ruddle 1998; Shashikant *et al.* 1998; Shashikant and Ruddle 1996; cf. Lei, Wang and Juan 2005). Thus, spatial and temporal gene expression pattern alterations are due to changes in the *cis*-regulatory region that redirect gene expression to new times (heterochrony) and/or places (heterotopy) through differential binding of proteins to the upstream elements.[170] These changes occur either through the modification of preexisting elements (including deletion) or through the origin of new regulatory elements (Carroll, Grenier

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[169] *Cis*-regulation can also occur at the 3' end of a gene or quite distant from the promoter region on the 5' side.

[170] We can also include ‘heterometry’ (change in amount) and ‘heterotypy’ (change in type) (Arthur 2000a, 2004b) but I will ignore them here. Heterotopy has not received as much attention as heterochrony (Zelditch and Fink 1996).

and Weatherbee 2001). Although many genes experience altered regulation in the origin of a phenotypic novelty, most explanations concentrate on a particular gene (or set of directly interacting genes) rather than detailing multiple genetic regulatory differences.

The spatial and temporal gene expression changes invoked either concern an existing single gene ('co-option') or the recruitment of a duplicate gene copy or paralogue ('duplication') (cf. Ganfornina and Sánchez 1999). Gene duplication, either individually or through whole genome duplication (Kellis, Birren and Lander 2004; Langkjær *et al.* 2003; Postlethwait *et al.* 1998), offers an 'intuitive' route to achieve the materials needed for the origin of new phenotypic features (Ohno 1970; Ohta 2003). The original gene function can be maintained either because the duplicate goes on to serve a new role (neofunctionalization) or the paralogues complement each other to mimic the original function (subfunctionalization), allowing for subsequent modular modification. Recent theory details how individual genes undergoing duplication and divergence might become subfunctionalized or neofunctionalized as an outcome of differential mutation in *cis*-regulatory regions, producing composite expression domains that are distinct from the pre-duplication pattern or ancestral function (Force, Cresko and Pickett 2004; Force *et al.* 1999; Lynch and Force 2000; Lynch *et al.* 2001; cf. Ohno 1970; Ohta 2003; Stoltzfus 1999).

Even though these kinds of explanations are not mutually exclusive, whether duplication type explanations from developmental genetics are utilized depends on the degree of gene and genome duplication (as well as the genetic and genomic organization) present in particular groups of animals, which is variable among different metazoan clades (Chiu *et al.* 2002; Málaga-Trillo and Meyer 2001; Wagner, Amemiya and Ruddle 2003). The early evolution of vertebrates, with its host of new distinct characters such as neural crest cells, head, and bone, has been an exemplar for duplication explanations because of the genome duplications and gene family evolution that appear to have occurred prior to the radiation of the vertebrate clade (Abi-Rached *et al.* 2002; Gu, Wang and Gu 2002; Holland 1998; Holland *et al.* 1994; Iwabe, Kuma and Miyata 1996; McLysaght, Hokamp and Wolfe 2002; Meyer and Schartl 1999; Ohno 1970; Pébusque *et al.* 1998; Shimeld 1999; Sidow 1992, 1996; Suga *et al.* 1999).

Evidence for co-option of structural genes has been illustrated most poignantly for vertebrate lens crystallins (Piatigorsky 1992, 1993, 1998; Piatigorsky and Wistow 1991; Xu *et al.* 2000). But much of the force behind arguments for the co-option of *regulatory* genes comes from evidence of their presence in the last bilaterian common ancestor (Ball *et al.* 2004; Finnerty 2003; Finnerty *et al.* 2004; Gauchat *et al.* 2000; Hayward *et al.* 2002; King, Hittinger and Carroll 2003; Kortschak *et al.* 2003; Kusserow *et al.* 2005; Müller *et al.* 1999; Wikramanayake *et al.* 2003). Early morphological diversification (e.g. Cambrian radiation) could have been the result of co-opting these preexisting regulatory genes into new spatial or temporal expression patterns (Erwin 1999; Erwin and Davidson 2002; Holland 1998; Knoll and Carroll 1999; Miyata and Suga 2001; Ohno 1996; Peterson, Cameron and Davidson 2000; Shubin and Marshall 2000; Valentine, Jablonski and Erwin 1999; Wilkins 2002, ch. 13). For example, regulatory genes that are mesodermal markers in triploblastic animals (bilaterians) are present and expressed in diploblastic animals (cnidarians) lacking mesoderm (Martindale, Pang and Finnerty 2004; Müller *et al.* 2003; Spring *et al.* 2002; Spring *et al.* 2000). The genetic tools were already in the 'toolkit' and the origin of morphological novelties occurred through a mix and match of these preexisting tools (Carroll 2001; Carroll, Grenier and Weatherbee 2001), otherwise termed 'evolutionary bricolage' (Duboule and Wilkins 1998).[171]

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[171] Extensive co-option of regulatory genes has also been demonstrated for echinoderms (Lowe, Issel-Tarver and Wray 2002; Lowe and Wray 1997; Wray and Lowe 2000).

We can summarize the structure of developmental genetic explanations of evolutionary novelty in the following table using the modification of an existing *cis*-regulatory element to allow for new spatial expression of an existing gene for illustration (Figure 6). This lets us see at a glance that the types of explanation are not mutually exclusive and can be used iteratively for different genes. An evolutionary novelty can be due to the co-option of *gene A* at a different time during development due to the modification of an existing *cis*-regulatory element *and* a new place of expression for a duplicated gene (*gene* B_2, where *gene B* → *gene* B_1 and *gene* B_2) through the *de novo* origin of a *cis*-regulatory element.

Type of Difference **Type of Explanation**	*Heterochrony*	*Heterotopy*
Co-option		*cis*-regulatory modification
Duplication		

Figure 6: Summary of Structure for Developmental Genetic Explanations of Innovation and Novelty

Changes in *cis*-regulatory elements necessarily involve other genes, both regulatory genes and downstream structural genes. Developmental genetic explanations of evolutionary novelties always implicate multiple genes, though these are not regularly noted.

Because these explanations of novelty invoke multiple genes, the notion of a pathway or regulatory network is immediately relevant (Wilkins 2002). The multiple interactions among genes in the process of expression regulation form an interconnected network (Arnone and Davidson 1997; Davidson, E. H. 2001; Davidson *et al.* 2002; Revilla-I-Domingo and Davidson 2003). One simplified model demonstrates that developmental 'circuits' usually come in two formats, emergent (or self-organized) and hierarchical (or programmed), with the former being more malleable and yielding more complex outputs with fewer components whereas the latter is capable of greater fine tuning (Salazar-Ciudad, Newman and Solé 2001; Salazar-Ciudad, Solé and Newman 2001). These studies also show a tendency for emergent networks to be replaced by hierarchical networks over time. Some have argued that Evo-devo should use GENETIC PATHWAY or GENETIC NETWORK as its major organizing concept (Wilkins 2002).[172] One major challenge is isolating the ordering of these pathway changes, especially whether regulatory genes 'lead' or 'follow' in the process of *cis*-regulatory modifications relevant to both co-option and duplication-then-recruitment phenomena utilized in developmental genetic explanations of evolutionary novelty (Chipman 2001; cf. Budd 1999).

Regulatory networks flag the final feature of developmental genetic explanations of evolutionary novelties: *modularity*. The joint deployment of gene signaling cassettes during development implies dissociable units ('modules') that can undergo modification without a radical effect on other units (i.e. with limited pleiotropic effects), thereby allowing for a greater range of viable, new variation to arise (Bolker 2000; Burian 2005; Carroll 2001; Gerhart and Kirschner 1997; Nelson 2004; Niehrs 2004; Raff and Raff 2000; Raff 1996; Schlosser and Wagner 2004; Von Dassow and Munro 1999; Wagner 1996; Wagner and Mezey 2004; Winther 2001; cf. Gregory 1935a). These modules can occur at a variety of organizational levels, from gene expression territories to cells to anatomical parts (Gatesy and Dial 1996; Gilbert and Bolker 2001; Hartwell *et al.* 1999; Khosla and Harbury 2001; Klingenberg *et al.* 2001; Minelli 1998; Raff and Sly 2000; Schlosser and Wagner 2004; Winther 2001). For example, individual eyespots on butterflies can be modified independently of other eyespots or morphological aspects

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[172] "The implicit claim is that this concept [of genetic pathways and networks] provides a useful framework not merely for the best-understood developmental processes in key model organisms and their nearest relatives, but, in principle, for *all* evolutionary developmental changes" (Wilkins 2002, 504). This would put a conceptual bias into the interdisciplinary interactions of Evo-devo (see Chapter 6).

of the wing (Beldade and Brakefield 2003; Beldade, Koops and Brakefield 2002b; Monteiro *et al.* 2003). Modularity in ontogenetic processes means that developmental genetic changes involving multiple gene expression domains have limited pleiotropic effects in the mapping relation between genotype and phenotype (Mezey, Cheverud and Wagner 2000; Wagner 1996). Explanations of evolutionary innovation and novelty do not require considering every other feature of a lineage of organisms.[173]

The developmental regulation of gene expression involves much more than *cis*-regulatory mechanisms (cf. Han, Szak and Boeke 2004; Hannon 2002; Hirotsune *et al.* 2003; Keegan, Gallo and O'Connell 2001; Maniatis and Reed 2002; Maniatis and Tasic 2002; Martens, Laprade and Winston 2004; Meister and Tuschl 2004; Schmitt, Prestel and Paro 2005; Stotz forthcoming; Surani 2001; Winkler *et al.* 2004; Wittkopp, Haerum and Clark 2004) but these have received less attention in developmental genetic explanations of evolutionary innovations and novelties. Other forms of molecular genetic explanation are possible, including differences in the translational regulation of genes, as has been observed in the case of yeast strains containing a prion (True and Lindquist 2000). This prion serves as a protein-based element of inheritance in *S. cerevisiae* by facilitating novel phenotypic variation through the suppression of normal translation termination sites during protein synthesis (Li and Lindquist 2000; True and Lindquist 2000). When present and active it confers the ability to generate more heritable phenotypic variation, especially if yeast colonies are subjected to variable growth conditions. Prion possession allows for an explanation of the origin of novel phenotypic variation through the 'release' of hidden genetic variation apart from transcriptional regulation (True, Berlin and Lindquist 2004). A similar mechanism involves heat shock proteins that fail to chaperone

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[173] Whether or not these developmental modules are also units of selection is a separate question (Brandon 1999; Schank and Wimsatt 2001; Winther 2001).

protein folding under certain stressful conditions, thereby permitting the expression of previously hidden genetic variation (Queitsch, Sangster and Lindquist 2002; Rutherford and Lindquist 1998). This may be a general feature of complex gene networks (Bergman and Siegal 2003). These studies aim to demonstrate how novel variation origin is possible *in general*, but are not directed at elucidating the origin of variation at *particular phylogenetic junctures*. This partially accounts for their neglect in explanations of particular innovations or novelties.

In summary, developmental genetic explanations of novelty follow a two-step procedure of establishing a particular pattern of homologies and then postulating an evolutionary transition in terms of differential spatiotemporal gene expression due to *cis*-regulatory element alterations. The pattern component is routinely executed using developmental regulatory genes in widely separated taxa, which has been criticized because it does not recognize the significance of the empirical phenomena underwriting the molecular paradox. Using structural gene expression in closely related taxa can circumvent some of these difficulties. The process component concerns changes in time (heterochrony) or space (heterotopy) of developmental regulatory gene expression through *cis*-regulatory region sequence evolution. This can occur through the co-option of existing genes or via duplication then recruitment. These types of explanation involve more than one gene and often concern signaling pathways or regulatory networks, which can also be understood as developmental modules or parts thereof.

5.3. Explaining the Origin of Vertebrate Jaws

5.3.1. Overview of the Problem and Phylogenetic Context

One area of interest from the early evolution of vertebrates that pertains to the problem agenda of innovation and novelty is the origin of vertebrate jaws (an evolutionary *novelty*).

Historically, extant jawless fishes (agnathans) such as lamprey and hagfishes were considered the 'primitive' vertebrate form. But the relation of fossil armored jawless fishes (such as ostracoderms), which had dermal bone, and cartilaginous elasmobranchs (e.g. sharks) confounded attempts to track an appropriate ancestor-descendant grouping for the origin of jaws (Bowler 1996, 206-218). There was widespread agreement with Haeckel's proposition that jaws are derivatives of the anterior gill arches in agnathans, which also represents the current majority opinion. Although the fossil record offers little evidence for understanding the transition from no jaws to jaws, morphology and comparative embryology indicate that gnathal elements are derived from the two anterior gill arches, which have been bifurcated and specialized into the jaw apparatus (Hall 1999a, 255-258; Mallat 1996; Stahl 1985, 93-94; but see Forey and Janvier 1993; Janvier 1996). Correlative with this is the origin of the endochrondal portions of the jaws from neural crest cells, linking the elaboration of the serially homologous gill arches with the fulcrum of vertebrate origins (Gans and Northcutt 1983; Northcutt and Gans 1983). Jaw diversity and evolution is also tightly coupled with patterns and mechanisms of skull development and evolution (Gans 1993; Hanken and Hall 1993), as well as innervations, musculature, and other relevant soft tissue elements (cf. Kent and Carr 2001).

Following the discussion in Section 5.2, the issue of explaining the origin of vertebrate jaws can be profitably split into two distinct foci. The first concerns the assessment of homologies between the craniofacial elements of agnathans and gnathostomes (*pattern*) whereas the second concerns ascertaining the origin of craniofacial variation that could lead to the transformation of ancestral 'non-jaw' features into 'jaw-like' structures (*process*), assuming selection is continually operating. One of the most problematic aspects of evolutionary pattern related to the origin of jaws is the relative position of gill arches to gills in agnathans and gnathostomes (Goodrich 1930). In extant agnathans the gill arches that serve as a support are located outside (lateral) of the gills themselves, which are found internal (medial) to the arches. In extant gnathostomes the gill arch is located medial to the gills, thus appearing in the exact opposite topology. Arguments have been mounted both in favor of lampreys losing their internal arches and gnathostomes losing their external ones (Carroll 1988; Janvier 1996; Mallat 1996) but minimally there is a lack of resolution in character polarity for assessing these homologies.

The most elaborate study to date included a variety of elasmobranch fishes (e.g. dogfish, leopard sharks, hammerhead sharks, ratfish) and chimaeroids, extinct agnathans (e.g. ostracoderms), as well as lampreys and hagfish (Mallat 1996). Homologies were proposed for cartilage, bone, muscles, and nerves in the pharynx, jaws, velum, lips, and mouth. Mallat concluded that the gills of agnathans and gnathostomes are homologous but the branchial arches are not. Instead, the extrabranchial cartilages found in sharks (but absent in teleosts) are homologous to agnathan external gill arches, thus indicating a vestigial remnant of the agnathan ancestral condition. The proto-gnathostome seemingly had *both* internal and external branchial arches, and the jaw apparatus was co-opted from the internal anterior set.

Mallat's core conclusion aligns with the most commonly held position on evolutionary process scenarios for the origin of the jaw apparatus; i.e., derivation through specialization of the most anterior set of serially homologous gill arches (first branchial arch or mandibular arch), with a subsequent recruitment of the second (hyoid) arch for structural support. The existence of relatively unspecialized gill arches in extant agnathans makes this appealing because it seems a natural evolutionary route to diverge and diversify serially homologous elements (Wagner 1996; cf. Gregory 1935a). This scenario requires a specific solution, such as Mallat's, to the question of gills and gill arch topology since it makes the agnathan gill arch/gill character state ancestral, thus requiring gnathostome loss of external gill arches.

A few researchers find this scenario unconvincing and advocate an alternative pathway via the transformation of a pumping velum-like structure as seen in larval lampreys, which is derived from similar embryonic sources in the first branchial arch (Janvier 1996). Cartilaginous elements supporting the velum, which had a role in both respiration and feeding, are elaborated into an endoskeletal jaw with first and second branchial arches being co-opted later for support. Thus, 'jaws were always jaws' and the evolutionary fusion of velar cartilage and first branchial arch skeletal elements erases the traces of the transition. The extension of this new mouth demanded a different kind of structural support, internal gill arches, which relaxed selection on the external ones such that they were eventually lost. Regardless of which scenario is preferred, there is a consensus that increased ventilation was initially critical and efficiency of hard prey capture become advantageous later (Mallat 1996; but see Kimmel, Miller and Keynes 2001).

The phylogenetic context for vertebrate jaw origins involves a population of agnathan ancestors from the early Ordovician or late Cambrian exhibiting some form of suction feeding and cephalic anatomical structures that could be co-opted and modified into a jaw apparatus. But there is little agreement about the nature of the ancestral agnathans, especially with only two extant agnathan groups (lampreys and hagfishes), or the timing of the initiation of jaw evolution (Janvier 1996). Most recent textbooks represent gnathostomes as closely related to one or more fossil agnathans (forktails, heterostracans, ostracoderms, anaspids) with lampreys wedged somewhere among these groups and hagfishes being more distantly related (Cowen 2000). Jawless fishes are found in the Ordovician and well represented throughout the Silurian and Devonian but are absent in the Carboniferous. Jawed fishes first appear in the fossil record of the early Silurian (Carroll 1988; Janvier 1996). Although traditional scenarios advocate a rapid extinction of agnathans in the presence of gnathostome fishes (Gregory 1951), both groups coexisted for ~75 million years.[174] The early Silurian appearance of well-formed gnathostomes leads most researchers to place the geological locus of jaw evolution in the early Ordovician (~490 mya) or late Cambrian (~510 mya) (Carroll 1988; Janvier 1996).

Several relevant questions arise when considering the phylogenetic juncture of the origin of jaws. First, how derived are lampreys and hagfishes (i.e. how confident can we be about generalizing *from* them *to* extinct taxa)? Many have assumed that their parasitic (lamprey) or scavenger (hagfish) lifestyles are derivative, though fossil lampreys and hagfishes that exhibit morphology similar to extant forms are found by the middle Carboniferous (Carroll 1988; Janvier 1996). This is compounded by the existence of a distinct larval stage ('ammocete') in lampreys that lasts upwards of three to four years and a metamorphosis that involves a reorganization of the entire head and pharynx. (Hagfish share some features of ontogeny with lampreys but develop directly.) Also, the cartilaginous skeleton of lampreys is non-collagenous in contrast to gnathostomes (Wright and Keeley 2001). Is the ammocete larva of lampreys a derived condition? Second, what is the relationship between extant and extinct agnathans? Molecular studies using 18S and 28S ribosomal DNA with maximum-likelihood methods unite lampreys and hagfishes as monophyletic (Mallat and Sullivan 1998; Mallat, Sullivan and Winchell 2001), but others nest lampreys within osteostracans and anaspids having hagfishes more distantly related (Forey and Janvier 1993; Janvier 1996; cf. Meyer and Zardoya 2003).

Both of these questions feed into the third issue, which concerns the appropriate ancestral anatomy that jaw origins should be modeled from. If extant agnathans are highly derived or

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[174] Hypotheses about gnathostomes driving most agnathans to extinction or long term trends towards an active and predatory lifestyle in the origin of gnathostomes are not well supported (Purnell 2001).

more distantly related than fossil agnathans, then they are less useful for reconstructing the relevant anatomical changes in the head to achieve a jaw apparatus. The opposite conclusion makes comparative anatomical and developmental genetic studies of extant agnathans quite pertinent (Kuratani *et al.* 2001). These questions are in a constant state of flux as recent fossil finds of early vertebrates from the Chengjiang fauna in China favor an affirmative answer to whether extant agnathans are relatively derived anatomically (Shu *et al.* 2003; Shu *et al.* 1999). Janvier argues that ostracoderms are the most appropriate near relative of gnathostomes based on a variety of shared derived characters (Janvier 2001), but the relevance of this for jaw origins is unclear. Many claims about precise anatomical transitions from fossil agnathan anterior branchial arches to a primitive jaw apparatus are simply not confirmable, if not problematic (Stahl 1985, 93-6), and the catalogue of diversity of skull morphology in both jawless and jawed fishes is breathtaking (Janvier 1993, 1996; Schultze 1993).

5.3.2. Developmental Genetics of Craniofacial Ontogeny

A full survey of vertebrate craniofacial ontogeny is not possible but recent reviews are available (Francis-West *et al.* 1998; Helms and Schneider 2003). The vertebrate hindbrain is the most ancient evolutionarily, where the transient segmented rhombomeres initiate very specific molecular cascades that differentially pattern the pharyngeal arch area and more anterior craniofacial features (Moens and Prince 2002; Prince 1998). Cartilage and bone formation occur differently in the head than elsewhere in the body primarily as a consequence of the unique molecular mechanisms involved in the migratory neural crest cells (NCCs) from which the bulk of craniofacial elements are composed (Couly, Coltey and Le Douarin 1993; Falck, Joss and Olsson 2000; Gross and Hanken 2005; Hall 1999b; Horigome *et al.* 1999; Kuratani, Horigome and Hirano 1999; Le Douarin and Kalcheim 1999; McCauley and Bronner-Fraser 2003; Olsson 2003; Olsson *et al.* 2001; Trainor, Melton and Manzanares 2003). Ectoderm derived cells from the region overlaying the neural tube that migrate both to 'cranial' and 'trunk' destinations were first identified by Wilhelm His in 1868. This was initially controversial because they transgressed the boundary of strict germ layer origin for features such as the spinal ganglia (Hall 1999b; Langille and Hall 1993; Trainor, Melton and Manzanares 2003).

NCCs are a major vertebrate novelty, not present in urochordates or cephalochordates, and their exact origin from ancestral chordate cellular forms is unknown (Gans and Northcutt 1983; Hall 1999b; Holland and Holland 2001; Holland *et al.* 2001; Meulemans and Bronner-Fraser 2002; Northcutt and Gans 1983; Shimeld and Holland 2000; Stone and Hall 2004; Wada 2001; but see Jeffery, Strickler and Yamamoto 2004). NCCs do not dictate particular morphological forms, as seen in derived vertebrates (such as anurans) that share developmental patterns of NCC migration and cell fates but yield novel cartilaginous and muscular elements (Olsson *et al.* 2001). With respect to the jaw apparatus, NCCs that populate the proximal mandibular arch skeleton in gnathostomes are derived from the both the 1st and 2nd rhombomeres,[175] whereas the distal elements are midbrain derived, and the most proximal region of the lower jaw is derived from 4th rhombomere NCCs of the second branchial arch (Köntges and Lumsden 1996; cf. Gross and Hanken 2005). Although the pattern in lampreys is conserved in many respects, key differences exist such as less specific and less ordered pharyngeal arch contributions and no NCC contribution to cranial sensory ganglia (McCauley and Bronner-Fraser 2003; cf. Horigome *et al.* 1999; Kuratani, Horigome and Hirano 1999; Langille and Hall 1993).

Since NCCs are the source for most of the cartilage and skeletal elements found in the head, a large number of developmental genetic studies have focused on them. The repression of

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[175] This assumes that the studies of chick embryos can be generalized (cf. Section 2.3.2.3 and 6.4.2.3).

Hox gene expression in NCCs fated for the anterior portion of vertebrate embryos is critical for normal skull morphogenesis, even though a typical collinear pattern is required of other NCCs to establish appropriate anterior-posterior axis specification of the remaining hindbrain portion (Moens and Prince 2002). Overexpression of *Hoxa2* or *Hoxa3* and *Hoxb2* in combination prevents the formation of the skull (Creuzet *et al.* 2002). NCCs receive instructive signals from their environment, specifically from foregut endoderm and hindbrain neural tube (rhombomeres) near the first branchial arch in the case of the anterior non-*Hox* expressing neural crest (Couly *et al.* 2002; Trainor and Krumlauf 2000), as well as from the oral epithelium for tooth development (Ferguson, Tucker and Sharpe 2000).[176] Thus, *Hox* gene expression is plastic, dependent on local signals in the cranial region during ontogeny, and a considerable amount of modularity exists in molecular processes operating during head development (Trainor and Krumlauf 2000).

A variety of other regulatory genes are involved in skull development. *Distal-less* (*Dlx*) genes, which exist in three, convergently transcribed pairs in vertebrates, are expressed in the forebrain portion of the neural tube and the ectomesenchymal cells derived from cephalic NCCs, as well as various surface ectoderm features such as appendages (Panganiban *et al.* 1997; Panganiban and Rubenstein 2002). They also exhibit a temporally sequential onset of expression during cranial development (*Dlx2*→*Dlx1*→*Dlx5*→*Dlx6*). Mice lacking *Dlx5* show a variety of craniofacial defects, including abnormalities in the anterior branchial arches (Acampora *et al.* 1999). *Orthodenticle* (*Otx*) and *Orthopedia* (*Otp*) genes are involved in brain development across a wide phylogenetic range of species (Acampora *et al.* 2000; Umesono, Watanabe and Agata 1999). *Otx2* mutants in mice exhibit distinct craniofacial malformations that include

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[176] This is in contrast to earlier experiments where explanted neural crest tissue grafted ectopically appeared to induce the fate of the tissue's origin. It has now been shown that this was a result of the donor tissue including the signaling center (the 'isthmic organizer'), which sends out a signal (FGF8) that (in part) negatively regulates *Hoxa2* expression (Trainor, Ariza-McNaughton and Krumlauf 2002).

lower jaw abnormalities (Hide *et al.* 2002). Bone morphogenetic proteins (BMPs) play a crucial part in craniofacial ontogeny, with evidence that *Bmp2/4* is required for normal cranial NCC formation and differentiation (Kanzler *et al.* 2000). The BMP antagonist *noggin* is involved in the formation of joints (Brunet *et al.* 1998; cf. Rountree *et al.* 2004), specifically having been shown to prevent cranial suture fusion (Warren *et al.* 2003). *Goosecoid* is found in many skeletal tissues and an analysis of the elements that compose the tympanic ring bone derived from mesoderm indicate that it is a cell autonomous factor in the recruitment and maintenance of an appropriate number of precursor cells in craniofacial condensations (Rivera-Pérez, Wakamiya and Behringer 1999). Sonic hedgehog (*shh*) has been implicated in an ectoderm signaling capacity for the correct patterning of the mid- and upper face regions (Hu and Helms 1999). *Shh* and *Fgf8* prevent programmed cell death and increase cell proliferation of NCCs that have migrated into the forebrain and frontonasal process (part of the mid- and upper face region) (Schneider *et al.* 2001).

A number of other candidate genes have been pursued via forward genetic analysis in zebrafish (Kimmel, Miller and Moens 2001). The *endothelin* pathway has a direct bearing on cartilage identity in the pharyngeal arches (Miller *et al.* 2000; see below). IκB kinase-α is critical for epidermal differentiation, which affects epithelial-mesenchymal interactions pivotal to craniofacial morphogenesis (especially the induction of mesodermal skeletal elements) through negative regulation of FGF family members (Sil *et al.* 2004). T-cell factor-3 (Tcf3) is a necessary inhibitor of Wnt signaling, which when mutated leads to an aptly named zebrafish mutant, *headless* (Kim *et al.* 2000). Cartilage morphogenesis and differentiation requires *sox9* activity, which in part initiates signaling that activates *col2a1*, a major cartilage collagen (Yan *et* *al.* 2002). Other homeobox containing genes such as *Msx-1* are also involved in patterning the developing face (Brown *et al.* 1993).[177]

Narrowing our focus to developmental genetic studies of vertebrate jaws *and* related structures in agnathans, most investigations of vertebrates concern three model organism systems (chick, mouse, and zebrafish) and candidate genes from these experiments have been studied in lamprey species (Kuratani, Kuraku and Murakami 2002), including the basics of agnathan cranial morphogenesis (Kuratani *et al.* 2001). These results are presented in a 'gene by gene' format before summarizing their role in explanations of vertebrate jaw origins.

5.3.2.1. *Distal-less* (*Dlx*)

Dlx genes were first demonstrated to play a critical role in the proximal-distal (or dorsal-ventral) patterning of the branchial arches in mice (Depew *et al.* 1999; Qiu *et al.* 1997; Qiu *et al.* 1995). These three duplicate pairs are expressed in a nested pattern in each branchial arch with *Dlx1/2* being expressed throughout, *Dlx5/6* from mid-arch through to the distal end, and *Dlx3/7* only in the distal region (Qiu *et al.* 1997). The sequential onset of these genes (*Dlx1/2*→*Dlx5/6*→*Dlx3/7*) shadows the spatial nesting. Inactivation of *Dlx5/6* in mice causes a homeotic transformation of the lower jaw into a second upper jaw (Beverdam *et al.* 2002; Depew, Lufkin and Rubenstein 2002), which is of interest because the asymmetry of vertebrate jaws is a derived condition. Both FGF8 and BMP4 have been implicated in the regulation of *Dlx2* in the first branchial arch mesenchyme and epithelium, respectively (Thomas *et al.* 2000).

Studies of *Dlx* family members in lampreys have yielded a different picture. Four *Dlx* cognates have been isolated from *Petromyzon marinus* and there is no obvious nested expression

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[177] I have discussed the developmental genetics of craniofacial ontogeny to the exclusion of gross anatomical descriptions, cell lineage studies, epigenetic aspects of differentiation and morphogenesis in the skull (Herring 1993; Thorogood 1993), and other supra-molecular details of head, face, and jaw development.

pattern in the branchial arches, where they are all strongly expressed (Neidert *et al.* 2001). Morphologically, there is no proximal-distal differentiation in lamprey branchial arches. These four paralogues show uncertain orthology to known *Dlx* genes in vertebrates, suggesting independent duplication events in these two lineages. In *Lampetra japonica*, one *Dlx* cognate has been isolated that shows close relations to *Dlx1* and *Dlx6* and is expressed in the forebrain and pharyngeal mesenchyme, later localizing to two sub-domains of the forebrain, upper lip and lower lip, and velar mesenchyme (Myojin *et al.* 2001). The forebrain expression is more anterior than any observed in gnathostomes studied thus far (Shigetani *et al.* 2002).

5.3.2.2. *Hox* (anterior group)

The key aspect of *Hox* gene expression for understanding jaw ontogeny is its *absence*. When anterior members of the *Hox* cluster (*Hoxa2*, *Hoxa3*, *Hoxb3*) are expressed in any NCCs that will contribute to craniofacial elements, severe malformations and complete absences of these skeletal units result, especially with respect to lower jaw components (Couly *et al.* 2002; Couly *et al.* 1998; Creuzet *et al.* 2002). The most posterior region of expression absence is the first branchial arch, which produces the bulk of the lower jaw, while the second branchial arch has a combination of anterior *Hox* member expression (Couly *et al.* 1998; Creuzet *et al.* 2002). The most anterior expressed *Hox* member (*Hoxa2*) has the most severe effect when expressed ectopically, inducing a full homeotic transformation of the first branchial arch into a duplicate second branchial arch in both chick and *Xenopus* (Grammatopoulos *et al.* 2000; Pasqualetti *et al.* 2000). Studies of *Hox* gene expression in one lamprey species (*Lampetra fluviatilis*) show an interesting break in co-linearity for middle group *Hox* members (*Hox5/6/7*), as well as expression in the most anterior gill arches (Cohn 2002). This result may be species specific, as no *Hox* gene expression is found in the branchial arches of *Lethenteron japonicum* (Takio *et al.* 2004).

5.3.2.3. *Fgf, Bmp,* and *Noggin*

FGFs and BMPs act in an antagonistic fashion (Neubüser *et al.* 1997) and *Fgf8*/*Bmp4* are primarily expressed in the ectomesenchyme of the pharyngeal arches, but not the more rostral portions of the head. They are involved in specifying the mandibular arch pattern and providing for NCC survival, distinguishing the maxillomandibular domain from the more rostral premandibular region (Shigetani, Nobusada and Kuratani 2000; Trumpp *et al.* 1999; cf. Kuratani *et al.* 2004). *Fgf8* and *Bmp4* regulate the expression of *Barx-1* and *Msx1* (Barlow *et al.* 1999; Trumpp *et al.* 1999), and *Fgf8* has also been shown to upregulate *endothelin-1* (Trumpp *et al.* 1999). *Fgf8* also induces rostral-caudal polarity within the first branchial arch, with rostral ectomesenchyme derived from NCCs differentiating into odontogenic cells while the caudal cells adopt a fate of distal lower jaw elements (Tucker *et al.* 1999). BMPs and retinoic acid in combination specify the maxillary components of the face in chick embryos, with overexpression of *noggin* (critical for joint formation) or retinoic acid leading to a transformation of maxillary elements into those of the frontonasal mass (Lee *et al.* 2001). Lamprey studies (*Lethenteron japonica*) of *Fgf8* and *Bmp4* cognates show expression patterns that indicate a conservation of signaling mechanisms but a shift in their topographical location (Shigetani *et al.* 2002; cf. Kuratani *et al.* 2004). Instead of being confined to the maxillomandibular region, expression extends rostrally into the post-optic region, which introduces ambiguity into comparisons of the oral regions in agnathans and gnathostomes. A different study of BMP2/4 related genes in *Petromyzon marinus* identified three cognate genes (only two were identified in *Lethenteron*) that likely arose from independent duplications, although the two putative lamprey orthologues show similar expression patterns (McCauley and Bronner-Fraser 2004).

5.3.2.4. *Otx* and *Emx*

Otx2 is involved in the formation of the lower jaw of mice (Francis-West *et al.* 1998; Hide *et al.* 2002). Two cognates of *Otx* have been isolated from *Lampetra japonica* (*OtxA* and *OtxB*) with *OtxA* showing putative orthology with gnathostome *Otx2* (Ueki *et al.* 1998). *LjOtxA* is expressed throughout the fore and midbrain, in the cephalic NCCs of the first branchial arch, as well as in the upper and lower lips along with *LjOtxB* (Horigome *et al.* 1999; Ueki *et al.* 1998). Another *Otx* cognate was isolated from a different lamprey species (*Petromyzon marinus*) and shown to be expressed initially in the presumptive fore- and midbrain, then later in the first pharyngeal pouch endoderm and mesenchyme, and resolves into a few narrow domains including the epidermal cells of the lower lip (Tomsa and Langeland 1999). *PmOtx* does not cluster with *LjOtxA* or *LjOtxB*, suggesting independent duplication events in lamprey lineages.

Emx is the vertebrate homologue of the arthropod gene *empty spiracles* and is expressed in the forebrain of gnathostomes but not in mesenchyme (Boncinelli, Gulisano and Broccoli 1993). In lampreys, a cognate *Emx* is expressed first throughout the neural tube but later is absent from myotomes and intensified in mandibular arch mesenchyme (Myojin *et al.* 2001). This pattern, which appears to be in the NCC derived ectomesenchyme, is unique to lampreys.

5.3.2.5. *Endothelin-1 / dHAND / Msx1*

Endothelin-1 (ET-1) is a small signaling peptide expressed in the epithelium and paraxial mesoderm of the branchial arches that initiates a cascade of molecular genetic events in the NCC branchial arch mesenchyme, including the upregulation of *dHAND*, which in turn modulates *Msx* expression (Charité *et al.* 2001; Miller *et al.* 2003; Thomas *et al.* 1998). dHAND is a helix-loop-helix transcription factor involved in maintaining NCC cells in the branchial arches, which undergo apoptosis when its expression is absent (Thomas *et al.* 1998), and patterning the first and second arches (Miller *et al.* 2003; Yanagisawa *et al.* 2003). Mutations affecting *ET-1* induce severe malformations in the craniofacial region of mice and mutations of *ET-1* in zebrafish, identified by the mutant *sucker*, have dramatic effects on the lower jaw and ventral (distal) pharyngeal arch cartilages (Miller *et al.* 2000), as well as bone (Kimmel *et al.* 2003). *ET-1* acts upstream of key branchial arch patterning genes such as *Dlx3*, *Dlx2*, *Dlx6*, *engrailed*, *dHAND*, *Msx1*, and *goosecoid* (Charité *et al.* 2001; Miller *et al.* 2003), including *bapx1*, which has been implicated in jaw joint formation (Miller *et al.* 2003).

5.3.2.6. *Pax*

A number of *Pax* paralogues have been isolated from *Lampetra japonica* and *Petromyzon marinus*, including groups *Pax2/5/8*, *Pax3/7*, *Pax1/9*, and *Pax6* (McCauley and Bronner-Fraser 2002; Murakami *et al.* 2001; Ogasawara *et al.* 2000). *LjPax6* is expressed in the oral and velar ectoderm, in addition to the eye, brain, and other head domains, while *LjPax2/5/8* is found at the mid-hindbrain boundary (similar to gnathostomes), as well as the mandibular arch (Murakami *et al.* 2001). *Pax1* and *Pax9* are expressed in the pharyngeal slits of gnathostomes (chick) with *Pax9* expression specifically in mandibular arch ectomesenchyme, whereas *LjPax9* first appears in the endoderm surrounding the first and future second pharyngeal pouches and then extends caudally over time into all of the pharyngeal pouches (Ogasawara *et al.* 2000). Later this pattern is restricted to the third through eighth arches but a new domain is found in the velar muscles, derived from the first branchial arch. *PmPax-7* and *PmPax-2* are expressed in ectodermal placodes, similar to gnathostome vertebrates (McCauley and Bronner-Fraser 2002).

5.3.2.7. *Engrailed*

Antibodies to the transcription factor Engrailed uniquely identify two specific jaw muscles in the developing cranium of zebrafish (the levator arcus palatini and the dilator operculi), although this expression is in mesoderm not derived from NCCs (Hatta *et al.* 1990). Using the same antibody in lampreys, it has been suggested that muscles of paraxial mesoderm rather than NCC origin are homologous to those having *engrailed* expression in zebrafish, and found in the anatomy of teleost fish more generally (Holland *et al.* 1993). These muscles are associated with velar pumping in the lamprey, seemingly favoring the scenario of the lamprey velum as a morphological precursor to the gnathostome jaw apparatus.

5.3.2.8. Caveat

Every pertinent developmental genetic expression pattern has not been reviewed here. For example, a *serrate*-like gene (*jagged2*) that encodes a ligand for Notch receptors is involved in the morphogenesis of the palate and targeted mutations reveal cleft palate phenotypes in mice (Jiang *et al.* 1998). Other relevant genes include *Alx4*, *Mhox*, *Pdgf-α*, *Pitx1*, *Prx2*, *Twist*, and *Wnt5a*, although their exclusion correlates with a relative lack of attention in the literature on jaw development and evolution, as well as the gap in our understanding of their functional roles (cf. Boorman and Shimeld 2002; Francis-West *et al.* 1998).

5.3.3. Summary of Explanatory Attempts

5.3.3.1. Pattern: Assessments of Homology

Related to our discussion of the problem of hierarchy in homology (Section 5.2.2.1), developmental genetic assessments of homology face a potential problem of circularity (cf. Hall 1999a). Consider the use of *engrailed* to establish homologies of lamprey velar muscles with the two jaw muscles that express *engrailed* in zebrafish (Hatta *et al.* 1990; Holland *et al.* 1993). Is the expression of *engrailed* alone in two derived species establishing homology of the higher-level structures (velar muscles and jaw muscles) or is *engrailed* marshaled as support for a homology assessment of these two structures on other grounds (relative position, embryological origin, etc.). Should we be cautious arguing, from *engrailed* expression patterns alone, that jaws arose from a velum-like structure in the ancestral agnathan ancestors of gnathostomes?

Patterns observed for *LjFgf8/17* and *LjBmp2/4* suggest complex homologies between the lower lips/mandibular arch in larval lampreys and gnathostome maxillary and mandible (mandibular arch derivatives) on the assumption of a heterotopic shift of epithelial-mesenchymal interactions (Shigetani *et al.* 2002). This assumes the ammocete larval form is ancestral. Those studying lamprey species have argued that many of the existing adult homologies between agnathans and gnathostomes may be obscured because of the massive alteration of NCC ectomesenchyme migration and location observed in lampreys.[178]

A different developmental hypothesis has been proposed to solve the reverse topographical relationship of gills to gill arches in terms of a differential migration of NCCs from an external or lateral position with respect to the gills to an internal or medial position

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[178] "Such mesenchymal rearrangements obliterate classically proposed one-to-one structural homologies in the adult state. Probably, the origin of the gnathostome jaw will not be found in any particular structures in lampreys or hagfishes. The velum would be homologous with the jaw only as a derivative of the mandibular arch, but neither of them would represent an ancestral condition of the other" (Kuratani *et al.* 2001, 1629; cf. Kuratani *et al.* 2004).

(Kimmel, Miller and Keynes 2001). Thus, the cartilages supporting gills in all vertebrates, agnathan and gnathostome, are homologous and no hypothesis is required with respect to an external loss/internal gain in gnathostomes or internal loss in agnathans (cf. Mallat 1996). This solution is similar to that proposed for the origin of external cheek pouches in geomyoid rodents, where a small change in tissue interactions during development induces the formation of a structure in the 'opposite' location (heterotopy), even though the structure itself forms nearly identically (Brylski and Hall 1988). Although the authors assume that the lamprey 'gills inside, arches outside' condition is ancestral, no independent evidence is brought in support of this. A developmental heterotopy of this nature erases its tracks and it would be difficult to sustain this argument without a functional demonstration of the consequences of altered lateral-medial NCC migration in the mandibular arch mesenchyme for agnathans and gnathostomes.

5.3.3.2. Process: Scenarios of Evolutionary Transition

A developmental genetic account of the molecular changes involved in the origin of jaws appears to have the following components:

- The restriction/absence of *Hox* expression from the anterior region of vertebrate embryos. The members of the first four paralogous groups of *Hox* genes do contribute to the hyoid bone of the second branchial arch, but any *Hox* expression in NCCs of the first branchial arch, from which the jaw develops, compromises the cartilage and skeletal elements.
- The duplication and divergence of *Dlx* genes into a nested proximal-distal pattern that differentiates the branchial arches. Other genes (e.g. *bapx1* and *dHAND*) involved in establishing this particular axial differentiation within individual arches fit into this scheme.
- *Fgf8* and *Bmp4* antagonistic signaling upstream of *Dlx* and *Msx* has been heterotopically shifted from a more expanded domain inclusive of the post-optic region in lampreys to a

maxillomandibular domain only in gnathostomes. This shift may have been a precondition for independent modification of the mandibular arch area.

- Several genes, including *Pax9* and *Emx* are likely important in the transition but their roles are currently only suggestive. Other genes such as *shh*, *wnt*, *sox9*, etc., may be important but remain obscure at the present time.
- Dissociation events that make putative markers misleading, such as *Fgf8* and *Bmp4* in the case of the lamprey and gnathostome upper lip, constrain accounts of structural transformation in the jaw apparatus.

There is little evidence of differences in *cis*-regulatory regions that may account for the differences between agnathan and gnathostome gene expression. Studies of *Dlx* paralogues primarily point toward conservation of regulatory elements (Sumiyama *et al.* 2002; Sumiyama and Ruddle 2003). Further isolation of candidate genes in lampreys is also required, *endothelin-1* being one of the more prominent because of its upstream role in activating multiple regulatory genes involved in jaw formation, especially for features not present in the lamprey such as jaw joints. These different gene expression patterns have not been routinely connected into a narrative of change at the level of a pathway or network but the modularity of some of the elements (such as branchial arches) is a critical aspect of these explanations.

Whether these explanations are co-option or duplication types depends on the particular gene family and evidence for duplication prior to the cyclostome/gnathostome divergence, although most researchers hold that duplication played a role (Holland 1998; Ohno 1970; Suga *et al.* 1999).[179] Duplication is a key part of the *Dlx* patterns but not for *Otx* because of independent

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[179] Early speculations on the role of regulatory gene alterations subsequent to gene duplication in the origin of novelty used vertebrate jaws as an example. "Since both the gill arch and jaws were made of bones, the change from one form to the other does not appear to have required the creation of new structural gene loci. But the modification appears to have required duplication of a regulatory gene or a group of regulatory genes which controlled gill arch development. First, the third gill arch had to be placed under separate control of a duplicated group of regulatory genes. Subsequent mutations may have changed the characteristics of these regulatory genes, so that the jaws were organized in place of a gill arch" (Ohno 1970, 87).

lamprey lineage duplications or for the repression of anterior *Hox* genes from the mandibular arch. The mutual compatibility of the different types of explanations is visible in this respect.

5.3.3.3. Other Considerations

Because the traditional hypothesis concerns the elaboration of anterior pharyngeal arches into a jaw apparatus, much of the developmental genetic research has concentrated on only these features. But others could be considered relevant for understanding vertebrate jaw origins when applying developmental genetic techniques. I briefly note three of them here: other pharyngeal arches, dentition, and muscles (as opposed to cartilage and bone).

The pharyngeal arches are of interest because these serially homologous features were extant long prior to the evolution of vertebrate jaws (Graham 2001a). Knowing the developmental genetic behavior of the arches that were *not* fundamentally altered may yield a helpful comparison when comprehending how the first and second branchial arches were transformed (Graham 2001a). Pharyngeal segmentation, which is present in cephalochordates, is not completely dependent on NCCs (Graham 2001b), consistent with studies already cited regarding the role of contextual cues for arch identities (Couly *et al.* 2002). Different regulatory genes and their downstream targets have been investigated in pharyngeal arch studies but not incorporated into developmental genetic studies of jaw origins. *Tbx1* interacts genetically with *Fgf8* in the fourth pharyngeal arch endoderm (Vitelli *et al.* 2002), the latter of which is critical for pharyngeal arch development, and also promotes NCC survival (Abu-Issa *et al.* 2002; Trumpp *et al.* 1999). A study of the FGF receptors in the pharyngeal region demonstrated that *Fgfr1* regulated the entry of migratory NCCs into the second branchial arch (Trokovic *et al.* 2003; cf. Francis-West *et al.* 1998).

For much of the past fifty years the origins of jaws and teeth were thought to coordinate but recent work calls this into question. Instead of skin denticles of dermal armor being internalized after or with jaw origination, vertebrates are held to have co-opted dentition from preexisting, internal pharyngeal denticles (Johanson and Smith 2003; Smith 2003; Smith and Coates 2001). Many of the molecular signaling cascades in tooth development are similar to those found in jaw development, such as the use of FGF and BMP signaling interactions (Neubüser *et al.* 1997), the expression of *Pax9*, *Dlx1/2*, *Shh*, *Barx1*, and others (McCollum and Sharpe 2001; Miletich and Sharpe 2003). The existence of several distinct, non-overlapping expression cascades are thought to corroborate the pharyngeal denticle hypothesis, with the 'jaw' gene patterns being co-opted in the origin of heterodonty (McCollum and Sharpe 2001). Attention is paid by dentition researchers to modeling the morphogenetic processes generating particular types of teeth (Reisz and Smith 2001; Smith 2003). This is partly a consequence of the exquisite preservation of teeth and their developmental history but research reconstructing fossil agnathan jaw morphogenesis is needed in addition to its molecular characterization.

A natural domain of intersection for jaw origins is jaw musculature, as opposed to cartilaginous or skeletal elements. Studies of regulatory genes undertaken thus far have focused on *engrailed* (see above). Structural genes specific to the jaw apparatus are also relevant, such as masticatory myosin (composed of a unique myosin heavy chain isoform), which arises only from the presomitic mesoderm of the first branchial arch (Hoh 2002). This uniquely jaw-expressed myosin is nicknamed 'superfast' because of its ability to contract with extreme rapidity in comparison to other myosins, such as in limb muscle fiber. It has been hypothesized that duplicates of pre-existing myosin heavy and light chain genes allowed for their recruitment and divergence into a jaw specific expression and function coordinately with the evolution of jaws

(Hoh 2002; Qin *et al.* 2002). The primary systems of study have been mammals (Qin *et al.* 2002) and few studies of masticatory myosins exist for fish taxa, which are critical for the phylogenetic juncture under consideration. A related study in a lamprey species isolated both muscle actin (*LjMA1* and *2*) and myosin heavy chain genes (*LjMH1* and *2*) from *Lethenteron japonicum* (Kusakabe *et al.* 2004). The following expression patterns were demonstrated: *LjMA2* in the upper lip primordia, lower lip, and more posterior pharyngeal arches early on with an expanding domain in oral, velar, and pharyngeal muscles later; *LjMA1* first appears in the cheek process, a likely source for skeletal muscles of the oral region and later is consistently and strongly found in the upper lip; *LjMyHC1* and *2* exhibited almost identical expression patterns in the developing myotomes and later throughout the myotomal skeletal muscles (but not in skeletal muscles originating from head mesoderm).

5.4. Explaining the Origin of Novel Embryonic Territories in Echinoids

5.4.1. Orientation and Scientific Background

Having seen several examples from vertebrate evolution, we turn now to an example from marine invertebrates.[180] The focus will be on the evolutionary pattern component of explanations of innovation and novelty, especially the establishment of non-homology in the absence of fossil forms for relatively recent evolutionary events. The origin of variation at a particular phylogenetic juncture is a function of developmental inaccessibility rather than phenotypic continuity. It involves a triangulation between an ancestral state of variation, a derived state of variation, and the absence of transitional fossil forms that speak to the nature of this difference. The connection between the two states of variation is one of qualitative

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[180] This section is excerpted from a longer manuscript on the topic (Love and Raff forthcoming).

difference that is the result of many different, nontrivial developmental changes (overcoming a developmentally inaccessible outcome). An epistemological gap exists regarding the developmental transition between these states of variation and the absent fossil forms. The following example of larval forms in sea urchins has occurred in the very recent past (~4mya) and concerns morphological features not documented in the fossil record. This example demonstrates how non-homology is operationally established in a concrete experimental system.

The origin and evolution of marine invertebrate larval forms is a key domain of research for evolutionary biologists (Strathmann 1978, 1985, 1993), including the repeated origin of direct developmental modes in echinoids, i.e. sea urchins (Hart 2002; Raff 1992; Wray 1996, 2000). Recent investigations have used molecular genetic techniques to unravel axis specification, cell fate, tissue differentiation, and signaling pathways in sea urchins (Angerer and Angerer 2003; Brandhorst and Klein 2002; Ettensohn and Sweet 2000). Maternal and early embryonic axial specification and patterning produce bilaterally symmetrical pluteus larvae that feed and grow in the water column. At metamorphosis, most larval structures are resorbed and the juvenile rudiment that arises through inductive interactions between a portion of the ectoderm (vestibule) and coelomic pouches on the left side of the animal begins to form adult morphological features (Okasaki 1975; Wray 1999b). A juvenile sea urchin emerges post-metamorphosis as a radially symmetrical individual, complete development, and settles into its benthic adult environment. This biphasic mode of development is labeled ‘indirect’.

Indirect developing sea urchins have two basic ectoderm territories, oral and aboral, that are established by the early gastrula stage from descendants of the animal half mesomeres and are demarcated by a ciliary band (Cameron and Coffman 1999; Hardin and Armstrong 1997; Okasaki 1975; Wray 1999b). Each territory has distinctive cell shapes (oral = cuboidal; aboral =

squamous) and are distinguishable by which end of the gut terminates into the territory (oral = mouth; aboral = anus). The oral-aboral axis that these ectoderm territories delimit is established zygotically and it coordinates with the first cleavage plane in some indirect developers (Cameron *et al.* 1989) but is variable in others (Henry, Klueg and Raff 1992; Kominami 1988). It is sometimes referred to as the larval dorsoventral axis (aboral=dorsal/oral=ventral).

Molecular studies have identified a variety of gene expression in one or the other territory that interact to produce exclusive oral and aboral territories along the larval dorsoventral axis (Amore *et al.* 2003; Angerer and Angerer 2003; Brandhorst and Klein 2002; Davidson, Cameron and Ransick 1998; Duboc *et al.* 2004; Ettensohn and Sweet 2000; Gross *et al.* 2003; Kenny *et al.* 2003; Takacs *et al.* 2004). The oral region exhibits higher respiratory activity that may contribute spatial information required in differentiating the ectoderm (Coffman and Davidson 2001; Coffman *et al.* 2004). A few genes are expressed in both territories but play a dynamic role in differentiating the ectoderm, such as *Otx* (Gan *et al.* 1995; Li, Wikramanayake and Klein 1999; Mao *et al.* 1996; Wikramanayake and Klein 1999), and *onecut* has been localized to the ciliary band (Poustka *et al.* 2004). Some are expressed in other territories during embryogenesis, such as *brachyury*, which has an earlier endoderm expression pattern followed by a 'secondary' domain of expression in the oral ectoderm at the mesenchyme blastula stage that resolves to the stomodeum and a ring around the anus (Croce, Lhomond and Gache 2001; Gross and McClay 2001; Rast *et al.* 2002). Ectoderm-expressed genes are involved in signaling to other territories to repress transcriptional activation and in determining specification of cell fate within the territory. Most of these cellular interactions are highly local in nature (Angerer and Angerer 2003; Hardin and Armstrong 1997) with a number of aspects of ectoderm differentiation being non-autonomously determined, including signals from the vegetal region of the embryo (Huang *et al.* 1999; Wikramanayake, Brandhorst and Klein 1995; Wikramanayake and Klein 1999). Other effects, such as calcium ion disruption, have been observed for the differentiation of oral from aboral ectoderm (Akasaka *et al.* 1997) and $NiCl_2$ treatment (Hardin *et al.* 1992).

The oral and aboral embryonic territories as defined by morphological landmarks and molecular markers are highly distinguishable entities and their ontogenetic individuation suggests they are legitimate developmental modules (Raff and Sly 2000). Therefore multiple criteria used to define modules can be applied (Raff 1996; Schlosser and Wagner 2004; Winther 2001), and they can be analyzed within frameworks available to account for the evolution of modules (Schlosser and Wagner 2004; Wagner 1996; cf. Gregory 1935a; see above, section 5.2.2.2). These territories are *conserved*, exhibit *individuality*, and are likely *unique* in the sense of characterizing a monophyletic group (Wagner 1989b).

5.4.2. The Problem of Ectoderm Differentiation in *Heliocidaris* Congenerics Differing in Developmental Mode

Two closely related sea urchin species from Australia in the genus *Heliocidaris* that differ radically in their developmental mode yet are phenotypically similar as adults diverged only approximately 4 mya (Zigler *et al.* 2003). *Heliocidaris tuberculata* is an indirect developing echinoid (Okasaki 1975; Wray 1999b), having the developmental features and ectoderm territory differentiation described above. This is the ancestral character state for echinoids (McEdward 1997; Strathmann 1978, 1985; Wray 1996). *Heliocidaris erythrogramma*, by contrast, has an ovoid shaped nonfeeding larval morphology and shortened time to metamorphosis termed ‘direct development’, which is facilitated by a dramatically larger egg (Raff 1992; Williams and Anderson 1975). It exhibits few overt morphological similarities with the pluteus larva, lacking appendages, an oral opening or functional gut, and possessing minimally vestigial skeletal elements and a reduced, interrupted ciliary band primarily involved in swimming (Emlet 1994, 1995). Evolution of its derived ontogeny has been rapid in contrast to the conserved developmental regulatory systems of indirect developers (Raff *et al.* 2003).

One developmental alteration involves the reorganization of ectoderm differentiation. The epithelium of a *H. erythrogramma* larva is a sheet of columnar cells dubbed 'extravestibular' ectoderm. The ciliary band forms a belt across the lower part of the ventral side of an individual and curves into non-connecting tips on the dorsal side (Emlet 1995). It marks the vestiges of both the oral-aboral axis and the oral and aboral ectoderm territories in the origin of any ectoderm regionalization in *H. erythrogramma* (Wilson, Andrews and Raff submitted). However, the large extravestibular territory appears to exhibit no regionalization and the ciliary band demarcates no territorial boundary (Raff and Sly 2000). The only demarcation of ectoderm that shows such differentiation is the left side vestibular ectoderm domain that emerges shortly after gastrulation, from which the adult rudiment will form through interactions with the hydrocoel, marking the precocious transition to metamorphosis (Williams and Anderson 1975).

Cell lineages of *H. erythrogramma* have been transformed with respect to the embryonic territories of indirect developers and do not offer obvious insight into the nature of the extravestibular ectoderm territory (Raff 1999a, 1999b). The basic question of homology concerns the relationship between the stereotypical oral and aboral embryonic territories in *H. tuberculata* and the extravestibular embryonic territory in *H. erythrogramma* (Raff 1999b). A vestibule forms much later in the ontogeny of indirect developers on the left side of the oral ectoderm, and thus if heterochronies for stereotypical events in indirect developing embryogenesis are applied to *H. erythrogramma* (Ferkowicz and Raff 2001; Parks *et al.* 1988;

Raff 1992; Raff *et al.* 1990; Raff and Wray 1989), the vestibular ectoderm in both species is directly related (i.e. they are homologous territories). Therefore, *H. erythrogramma* is considered to have a single larval ectoderm territory (the 'extravestibular' ectoderm) containing an interrupted ciliary band but without overt differentiation of oral or aboral ectoderm. Additionally, cross-species hybrids in which *H. erythrogramma* eggs are fertilized by the sperm of *H. tuberculata* (Raff, E.C. *et al.* 1999) yield territory information as the resulting hybrid embryos produce a pluteus-like morphology and exhibit recognizable territories with gene expression, including an oral ectoderm (Nielsen *et al.* 2000).

Analyzing the relationship between these molecularly and morphologically defined territories (or modules) in *H. tuberculata* and the ectoderm territories (or modules) of the direct developer *H. erythrogramma* permits judgments of homology and evolutionary alterations for the territories.[181] To ask how these ectoderm territories are homologous, if at all, a review was undertaken of the molecular and morphological evidence concerning the ectoderm in each species (Table 1 and Table 2). Seven morphological characters can be identified (Table 1).

1. Extravestibular ectoderm cells of *H. erythrogramma* are columnar, not either the cuboidal oral ectoderm cells or squamous aboral epithelium (Nielsen *et al.* 2000).
2. Different larval structures exhibit distinct fates at metamorphosis (Chia and Burke 1978). Aboral ectoderm in indirect developers is resorbed and the extravestibular ectoderm in *H. erythrogramma* shares a similar fate (Haag and Raff 1998).
3. Neural cells arise exclusively from the oral ectoderm of indirect developers (Bisgrove and Burke 1987; Nakajima *et al.* 2004), including *H. tuberculata* (Bisgrove and Raff 1989). Neural cells arise in the extravestibular ectoderm of *H. erythrogramma* (Bisgrove and Raff 1989; Sly 2004), implying a shared feature with the oral ectoderm.

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[181] That is, the *joint* use of molecules and morphology individuates germ layer territorial divisions as developmental modules, which can then be assessed for homology at a particular level of organization (Minelli 1998, 2003a).

4. The beginning of the formation of the adult rudiment in indirect developers involves a flattening of part of the oral ectoderm on the left side (the vestibule) where the left coelom will make physical contact (Okasaki 1975; Wray 1999b). The vestibule of *H. erythrogramma* arises on the left side of the extravestibular ectoderm, implying a feature shared with the oral territory (Ferkowicz and Raff 2001; Haag and Raff 1998).
5. An oral opening appears in the oral ectoderm and an anal opening appears in the aboral ectoderm of indirect developers. The blastopore of *H. erythrogramma* closes shortly after primary invagination and no epithelial invaginations occur until vestibule formation.
6. The ciliary band demarcates the boundary between oral and aboral territories in indirect developers, including *H. tuberculata*. The ciliary band of *H. erythrogramma* demarcates no discernable territory.
7. Larval arms extend from the epithelium traversed by the ciliary band and are composed of both oral and aboral ectoderm. *H. erythrogramma* has no larval arms.

Ectoderm gene expression patterns in the two developmental modes differ (Table 2) and the patterns fall roughly into four categories:

I. Gene expression stereotypically found in oral or aboral ectoderm of *H. tuberculata* is either present or absent in the extravestibular ectoderm of *H. erythrogramma*: *EctoV* (Raff, E.C. *et al.* 1999), *Arylsulfatase* (Haag and Raff 1998), *14-3-3ε* (Love, Lee and Raff in preparation), *Msx* (Wilson 2003; Wilson, Andrews and Raff submitted), neural peptides (Love and Raff, unpublished observations; Sly *et al.* 2002; Sly 2004).

II. Gene expression found in both oral and aboral ectoderm territories is also observed in the extravestibular ectoderm of *H. erythrogramma*: *CyIa*, *EGFI*, *EGFIII*, *Otx*, and *Runt* (Bisgrove, Andrews and Raff 1995; Kissinger and Raff 1998; Nielsen *et al.* 2003; cf. Morris *et al.* 2004).

Table 1: Comparisons of Morphological Features Relevant for Ectoderm Territories

Each morphological feature is scored for its presence or described with respect to the oral and aboral ectoderm of *H. tuberculata* and the extravestibular ectoderm of *H. erythrogramma*. The final column compares these and scores the result in one of three ways: Aboral = extravestibular ectoderm feature matches aboral ectoderm feature; Oral = extravestibular ectoderm feature matches oral ectoderm feature; Unique = extravestibular ectoderm feature matches neither the oral or aboral ectoderm feature.

Morphological Feature	***Ht* Oral Ectoderm**	***Ht* Aboral Ectoderm**	***He* Extravestibular Ectoderm**	***He* vs. *Ht* Comparison**
Cell Shape	Cuboidal	Squamous	Columnar	Unique
Fate at Metamorphosis	Reassociated into adult structures	Resorbed and hydrolyzed	Resorbed and hydrolyzed	Aboral
Origin of Neural Structures	Yes	No	Yes	Oral
Vestibule	Yes (left side)	No	Yes (left side)	Oral
Oral/Anal Opening	Yes	Yes	No	Unique
Ciliary Band	Boundary	Boundary	Not boundary	Unique
Larval Arms	Yes (part)	Yes (part)	No	Unique

Table 2: Comparisons of Gene Expression Relevant for Ectoderm Territories.

Each gene expression pattern is scored for its presence and nature with respect to the oral and aboral ectoderm of *H. tuberculata* and the extravestibular ectoderm of *H. erythrogramma*. They are then compared and scored in one of three ways: Aboral = extravestibular ectoderm expression matches aboral ectoderm expression; Oral = extravestibular ectoderm expression matches oral ectoderm expression; Unique = extravestibular ectoderm expression matches neither the oral or aboral ectoderm expression. Expression found in all of the territories is not scored (—). If the key difference is the presence or absence of highly localized expression in a distinct region of the ectoderm territory, this is noted with 'localized' or 'not localized'. * indicates an expression pattern inferred from another indirect developing species.

Gene Expression	***Ht* Oral Ectoderm**	***Ht* Aboral Ectoderm**	***He* Extravestibular Ectoderm**	***He* vs. *Ht* Comparison**
EctoV	Yes	No	No	Aboral
EGFI	Yes	Yes	Yes	—
EGFIII	Yes	Yes	Yes	—
CyIIIa	No	Yes	No (pseudogene)	Unique
CyIa	Yes	Yes	Yes	—
Apextrin	No	No	Yes	Unique
HeEl	No	No	Yes	Unique
Arylsulfatase	No	Yes	No	Oral
Advillin	No	No	Yes	Unique
Flotillin	No	No	Yes	Unique
14-3-3ε	Yes	No	Yes	Oral
Otx	Yes	Yes	Yes	—
Goosecoid	Yes	No	Partial	Unique
Otp	Yes (localized)	No	Yes (not localized)	Unique
Msx	Yes	No	No	Aboral
Runt	Yes	Yes	Yes	—
Brachyury	Yes*(localized)	No	Yes (not localized)	Unique
Neural peptides	Yes	No	Yes	Oral

III. Gene expression exhibiting a very focused pattern (small subset of cells or region) in *H. tuberculata* ectoderm is expressed throughout the ectoderm of *H. erythrogramma* with no particular locus of intensity: *Otp* (Zhou *et al.* 2003), *Goosecoid* (Wilson 2003; Wilson, Andrews and Raff submitted; Wilson *et al.* in preparation), and *Brachyury* (Nielsen and Raff, unpublished observations).[182]

IV. Novel gene expression is observed in the extravestibular ectoderm of *H. erythrogramma* that is not found in either ectoderm territory of *H. tuberculata*: *Apextrin* (Haag and Raff 1998; Haag *et al.* 1999), *CyIIIa* (Kissinger, Hahn and Raff 1997; Kissinger and Raff 1998), *HeEl* (Haag and Raff 1998; Haag *et al.* 1999), *Advillin* (Love, Andrews and Raff in preparation), and *Flotillin* (Love, Lee and Raff in preparation).

5.4.3. Vestibular Ectoderm in *H. erythrogramma* is an Evolutionary Novelty

The unspecified ectoderm as one of the three primary germ layers is unquestionably homologous between each of the *Heliocidaris* species (cf. Hall 1998). Thus, there is embryological homology prior to ectoderm differentiation in early development but it becomes more difficult to track territory identities shortly thereafter. Given the extensive alterations that have been documented in the early development of *H. erythrogramma*, as well as larval morphology differences, the high degree of similarity in the adult morphology of these two sister taxa points to remaining homologues that maintain the developmental trajectories and outcome of the adult sea urchin. The vestibular ectoderm and the complex structure of the rudiment are good candidates. Both species have a vestibule and a rudiment that forms through interactions between the coelomic pouches and vestibular ectoderm to eventually produce the adult sea urchin via metamorphosis (Minsuk and Raff 2002). The 'direct' development observed in *H. erythrogramma* is relative to the maximal indirect development of other euechinoids because it

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[182] The expression pattern of *brachyury* in *H. tuberculata* has not been determined but is inferred to be similar to other indirect developers.

still retains a biphasic life history, the transition of which is marked by metamorphosis from an echinus rudiment in a highly stereotypical fashion despite a radically altered larval morphology.

The presence of extreme heterochronies in the onset of vestibular ectoderm formation has partly occluded these insights because several of the genes that are expressed in the oral ectoderm of indirect developers show expression in vestibular ectoderm, encouraging a comparison of the oral or aboral ectoderm with the vestibular ectoderm. If one considers a unified sequence of developmental events (Reiss 2003; Smith 2002) in an indirect developer (fertilization [F], ingression of mesenchyme [I], gastrulation [G], oral/aboral ectoderm differentiation (O/A), neurogenesis initiation (N), vestibule formation (V), rudiment formation [R], metamorphosis [M]) and assume the division of the ectoderm into vestibular and extravestibular ectoderm [E/V] is similar to oral/aboral ectoderm differentiation in *H. erythrogramma*, the following ordering of development events is adduced (ignoring actual time to completion of these events):

H. tuberculata: F, I, G, O/A, N, V, R, M
H. erythrogramma: F, I, G, E/V, R, N, M

But if we split the two phases of development and ignore the onset time of the events, the confounding nature of heterochronies is removed because the temporal collapse of events from the different developmental phases of *H. erythrogramma* can be explicitly recognized (e.g. adult vestibule formation being prior to larval neurogenesis).

H. tuberculata: Embryonic/Larval: F, I, G, O/A, N Adult: V, R, M
H. erythrogramma: Embryonic/Larval: F, I, G, E, N Adult: V, R, M

What emerges as distinctive from this event sequence comparison is a lack of *larval* ectoderm differentiation into *two* distinct territories around the end of gastrulation in *H. erythrogramma*. Describing ontogeny as discrete stages requires an assumption of causal connection between the stages (Alberch 1985; cf. Minelli 2003a; Reiss 2003; Smith 2002). Separating the ordering of events by phases of development is legitimate because they are largely independent, unlike the stages within a developmental phase. The differentiation of ectoderm into oral and aboral territories is causally connected with the generation of pluteus morphology in indirect developers and thus a lack of differentiation into these two distinct territories alters the larval morphology of *H. erythrogramma* in a dramatic fashion. In contrast, the causal processes required for vestibular ectoderm differentiation and rudiment formation for the second developmental phase (once initial specification has occurred in the larval stage) appear to be decoupled from the former indirect larval stages (Minsuk and Raff 2002).

The morphological and molecular data shown in Tables 1 and 2 yield no straightforward way to homologize the oral or aboral ectoderm with the extravestibular ectoderm, consistent with the lack of differentiation into two distinct territories in the first phase of the life history of *H. erythrogramma*. Although two morphological features (origin of neural cells and vestibule formation/location) favor a relationship of the extravestibular ectoderm with oral ectoderm, and one feature (metamorphic fate) favors the reverse relationship, four of the morphological landmarks are unique. Eight of the sixteen gene expression patterns are either novel or radically altered in *H. erythrogramma*, whereas three of the five patterns that imply either an oral or aboral sameness assessment are due to absence rather than presence of expression. At best, assigning a relationship of homology for the extravestibular ectoderm of *H. erythrogramma* to either the oral or aboral ectoderm is ambiguous. If these ectoderm alterations are represented in a schematic phylogeny with an indirect developing euechinoid outgroup (cf. Littlewood and Smith 1995; Philip 1965; Smith 1988, 1989; Zigler *et al.* 2003), the collection of 'apomorphies' leads naturally to the conclusion that the ectoderm territory of *H. erythrogramma* is novel; i.e. not homologous (Figure 7; Müller and Wagner 1991). A hypothesis of the different relationships of homology throughout the ontogeny of *H. tuberculata* and *H. erythrogramma* are pictorially represented in Figure 8, showing both the retention of key homologues (e.g. vestibule) and the lack of homology between ectoderm territories.

The negative assessment of homology between the ectoderm territories of these two species remains even when a variety of other phenomena (reversals, rudiments, vestiges, atavisms, and parallelism) are recategorized under the concept of homology (Hall 2003a) because the extravestibular ectoderm territory in *H. erythrogramma* is not itself a vestige, even though other characters, such as gene expression, can be considered vestigial. This hypothesis leads to a putative mechanistic scenario (*process*) for the evolution of the ectoderm territories from indirect to direct development that can be correlated with the putative morphological transitions in larval forms previously postulated (Wray 1996). Two definable modules have been restructured into a single new ectoderm territory, the extravestibular ectoderm, through a process of destabilization during the loss of the ability to feed and consolidation during the reduction of pluteus larval morphology. The vestibule remains as an organizing unit along with rudiment formation in the second phase of development, thereby accounting for the similarity in adult morphology (cf. Love and Raff forthcoming).

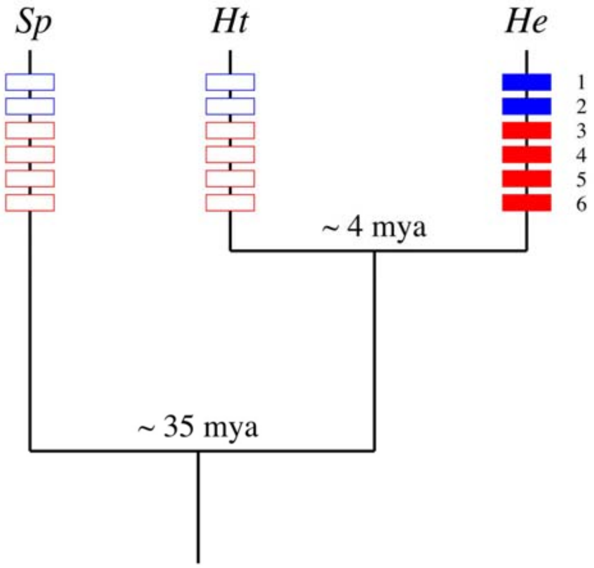

Figure 7: Phylogenetic Distribution of Ectoderm Characters

1: Unique ectoderm gene expression; 2: Highly modified ectoderm gene expression; 3: Cell Shape; 4: Absence of oral/anal opening; 5: Ciliary band not a boundary; 6: No larval arms

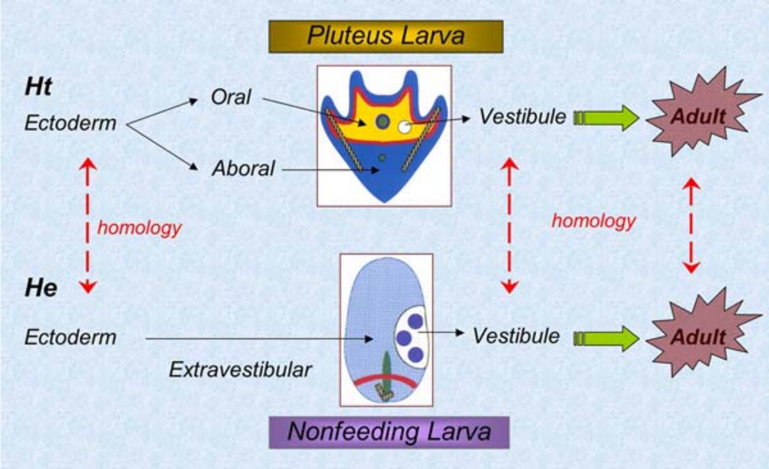

Figure 8: Overview of Larval Homologies in *Heliocidaris*

Key homologies are marked with red arrows: undifferentiated ectoderm, vestibular ectoderm, and adult phenotypic structures. Note that there is no inferred homology relationship between the oral or aboral ectoderm of the pluteus larva of *H. tuberculata* (*Ht*) and the extravestibular ectoderm of *H. erythrogramma* (*He*).

5.4.4. Postscript on Primary Case Studies

The case studies above (origin of vertebrate jaws and ectoderm territories in sea urchins) are not simply two exemplars of attempts to explain evolutionary novelties from a developmental genetic perspective. They also highlight different stages in the process of identifying and explaining these novelties. In the case of the origin of vertebrate jaws, *that* vertebrate jaws are evolutionarily novel has long been accepted and thus developmental genetic explanations, whether concerning pattern or process, are injected into a longstanding problem context to unravel how they originated. But in the case of the extravestibular ectoderm territory of *H. erythrogramma*, the determination *that it is an* evolutionary novelty is new, there is therefore less material bearing on the possible process of transition from a developmental genetic perspective, although some recent work addresses the issue (Wilson, Andrews and Raff submitted). The advantage of using these two examples is to show how specific empirical problems can be in different stages of evaluation and thus the way in which developmental genetic type explanations can be utilized also slightly differs.

5.5. From a Different Angle: Alternate Explanatory Approaches

A variety of other 'ways' of explaining innovation and novelty remain in contemporary biology. Capturing the outlines of these alternate explanatory approaches will allow for comparison and contrast when it comes to reconstructing conceptual clusters used to explain the origin of novel features. Plant biology is ignored for space considerations (as in Chapter 4)[183] as

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[183] Explanations of novelty in plants use molecular developmental genetic methodology and are similar to the animal examples (but see Endress 2001; Frohlich 2003). The origin of flowers has been studied most intensely (Baum *et al.* 2002; Gutierrez-Cortines and Davies 2000; Honma and Goto 2001; Keck *et al.* 2003; Kramer and Irish 1999, 2000;

is systematics because it does not offer causal explanations of novelties, although it is critical in establishing pattern-based aspects of the problem to be solved (Telford and Budd 2003).[184]

5.5.1. Population and Quantitative Genetics (or Evolutionary Genetics)

Population genetics has been at the core of evolutionary theory since the Modern Synthesis and quantitative genetics has been increasingly utilized in evolutionary analysis in recent decades. They can be collected under the phrase 'evolutionary genetics' (Ridley 2004, ch. 5-9). At first blush, the route to novelty at the genic level is mutation. But this is not a *qualitative* departure from the ancestral condition, only an allelic variant (orthology being readily apparent). Researchers using population genetic models have recognized this issue.

> The process of adaptation occurs on two timescales. In the short term, natural selection merely sorts the variation already present in a population, whereas in the longer term genotypes quite different from any that were initially present evolve through the cumulation of new mutations. The first process is described by the mathematical theory of population genetics. However, this theory begins by defining a fixed set of genotypes and cannot provide a satisfactory analysis of the second process because it does not permit any genuinely new *type* to arise (Yedid and Bell 2002, 810, my emphasis).

Population genetics concerns the dynamics of existing genotypes and gene frequencies but does not address the mechanistic origin of new genes *per se*.

Quantitative genetics can be thought of as a phenotypic counterpart to the population genetic analysis of genotypes (cf. Lynch and Walsh 1998). Morphological features that vary quantitatively are measured and a numerical value for selection can be extracted based on the

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Lawton-Rauh, Alvarez-Buylla and Purugganan 2000; Lawton-Rauh, Buckler and Purugganan 1999; McSteen *et al.* 1998; Pelaz *et al.* 2000; Soltis *et al.* 2002; Theißen and Saedler 1999; Vergara-Silva, Martíne-Castilla and Alvarez-Buylla 2000; Vijayraghavan 2001; Weigel and Meyerowitz 1994; Winter, Saedler and Theißen 2002; Winter *et al.* 2002; Yun, Weigel and Lee 2002), whereas leaf morphology has received less attention (Beerling, Osborne and Chaloner 2001; Harrison *et al.* 2005; Tsiantis and Hay 2003). See also Friedman and Carmichael 1998; Graham, Cook and Busse 2000; Vergara-Silva 2003; Walker Larsen and Harder 2001.

[184] But even in the case of the pattern component, phylogenetic reconstruction is not sufficient as the discussion of ectoderm territories in echinoids illustrates.

variation behavior of these features across generations. The primary assumption is that population variances for these characters are controlled by many (unknown) genes (V_G). Environmental factors also affect character variation (V_E), as well as interactive effects between these genes and the environment (V_{GxE}). Thus, the variance observed for a particular morphological feature in a population is $V_G + V_E + V_{GxE}$. Note that variance is not equal to variation. The statistical measure of deviation from a mean population value (variance) is not the same as the variation that exists in a population. Our concern throughout this study has been with the origin of variation at particular phylogenetic junctures, not variance.

An assumption of population genetic theory (as understood in the Modern Synthesis) is that the allelic variants that arise due to mutation have phenotypic effects that can eventually *lead to* the origin of evolutionary innovations and novelties (cf. Stern 2000). Objections to thinking of the problem of explaining evolutionary novelties as something other than "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, 357) largely arise from conceptualizing the problem in terms of phenotypic continuity (gradualism versus saltationism) rather than alterations in genotype-phenotype relationships (developmental accessibility) (cf. Charlesworth 1990; Charlesworth, Lande and Slatkin 1982).[185] Quantitative genetics arguments focus on the possibility of gradual shifts from one phenotypic peak in an adaptive landscape to another (i.e. from one character to a qualitatively different one) (Benkman and Lindholm 1991; Lande 1986; Price, Turrelli and Slatkin 1993). Since this *requires* that the intervening phenotypes are developmentally accessible, energy has been devoted to showing that

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[185] The technical manifestation of this conceptualization is that representational structures in the mathematical models of quantitative genetics (e.g. metric or vector spaces) represent phenotypic space as abstract, continuous surfaces implying that movement through these spaces is only constrained by fitness criteria (e.g. peaks and valleys) (Stadler *et al.* 2001; cf. Arthur 2004a; Phillips and Arnold 1989). Another difficulty is the neglect of determining whether a derived feature is non-homologous with an ancestral feature (see, e.g., Benkman and Lindholm 1991).

no developmental constraints exist or, if they do, they can be overcome via selection or random genetic drift given enough time (Arnold 1992; Charlesworth, Lande and Slatkin 1982; Cheverud 1984, 1990; Lande 1986; Levinton 1986; Scharloo 1990; cf. Slatkin 1987; Wagner 1988).[186] Theoretical investigations show that mutations of large effect are not necessarily more deleterious than those of small effect (Orr 1998; cf. Clarke and Arthur 2000; Stern 2000), contrary to predominant Fisherian theorizing of the 20th century (Charlesworth 1990). Pleiotropic effects can be confined to particular phenotypic modules, such as in the mouse mandible (Atchley 1987; Atchley and Hall 1991; Cheverud 2001, 2004; Mezey, Cheverud and Wagner 2000).

Some authors have argued that accepting a distinct explanatory burden for innovation and novelty is evidence of typological thinking (i.e. not thinking of population level variation).

> A substantial portion of the key innovations noted in the evolutionary literature are typological constructs. Empirically they do not represent true evolutionary innovations, and as such are limited in what they can tell us about the processes actually responsible for the origin and maintenance of evolutionary novelties. The ontological mistake has arisen because the analysis of evolutionary innovation has largely been confined to hierarchical levels well above that at which processes producing innovations have operated. … manifestations of pattern above the level of differentiating populations, or basal taxa, are epiphenomena, or effects, of lower level processes (Cracraft 1990, 23).

We recognized the significance of different hierarchical levels in Chapter 2, where the issue was not whether innovations or novelties are typological constructs but the difficulty in understanding what combination of form and function features at different hierarchical levels need to be compositionally or procedurally present for the feature to originate in developmental space and evolutionary time.[187] Rather than typology, recognizing the hierarchical complexity of

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[186] Quantitative genetic studies demonstrating the effects of natural selection on the *diversification* of particular traits does not address the *origin* of a qualitatively new trait (cf. Rieseberg *et al.* 2002).

[187] Thus, the 'ontological status' of innovations or novelties is not as significant as Cracraft argues. For example, his specific complaint about avian flight has already been dealt with in our discussion of the 'many structures to one

form and function features calls into question the assumption of a transparent genotype-phenotype map, which holds that allelic variants at the genic level translate into phenotypic variation in a straightforward or linear manner.

Although some proponents of evolutionary genetic approaches proceed by denying the problem agenda presupposition that these variation phenomena are genuine (phenomena are *typological*) or distinct (phenomena are only *quantitatively* different), others have offered analytical tools that are sensitive to ontogeny. Studies of the connection between developmental processes and quantitative variation are suggestive but still in their infancy (e.g. Rice 1998, 2000; Wolf *et al.* 2001). One controversial proposal using population genetic parameters argues that mutations in homeobox genes could arise in a recessive state, spread in a population (via standard population genetic dynamics), and later have a qualitatively distinct phenotypic effect in multiple individuals allowing for the propagation of the recessive, homozygous genotype responsible for the new feature (Schwartz 1999a, 1999b). Population biological studies have implicated hybridization in the origin of novel color patterns in snails (Chiba 1993, 1997), although the application of hybridization to other morphological features is much less clear.[188] Arthur has tried to connect population studies of centipede segment number variation (intraspecific) with known developmental genetic information about arthropod segmentation

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function' feature found in attempted explanations of evolutionary innovations in chapter 3 (Section 3.3.5). "[It] is readily apparent that the key innovation [avian flight] just discussed lacks any ontological status as an evolutionarily discrete novelty. Avian flight, even if it could be said to characterize modern birds, is composed of very large suite of characters that arose within the avian clade at very different times, extending over perhaps 50 millions years or more. In addition, many of the "character" just discussed are undoubtedly themselves aggregates of characters, which arose at different times" (Cracraft 1990, 26). What Cracraft labels 'ontological status' is part of the explanatory burden concerning evolutionary innovation and novelty. That is, it is *epistemological*, not ontological. On the analysis offered here, part of Cracraft's main desiderata is fulfilled: "the correct domain for studying innovation is between the molecular (processes of mutation and development) and populational (processes of differentiation) levels and that the approaches brought to bear on the problem of innovation will depend upon the questions asked and the focal level to which they are directed" (28). The key difference is the exclusion of diversification subsequent to the origin of a feature (i.e. key innovation).

[188] Studies of interspecific hybridization in plants have implicated the process in the origin of numerous features related to speciation events (e.g. Rieseberg *et al.* 2003). Tenuous arguments have been offered for the origin of larval forms via interspecific hybridization but they have not been experimentally verified (Williamson 2001, 2003).

(Arthur 1999, 2000b; Arthur and Farrow 1999; Arthur and Kettle 2001). The primary difficulty is that geophilomorph centipedes are not being studied with developmental genetic tools. The information about segmentation ontogeny is inferential, drawn from insects and crustaceans.

Wade and Goodnight have claimed that "the central problem of evolution for Wright was explaining the origins of adaptive novelty, whereas for Fisher it was explaining the refinement of existing adaptations" (Wade and Goodnight 1998, 1540; cf. Toquenaga and Wade 1996) but the meaning of 'adaptive novelty' is different than explaining the origin of evolutionary innovations and novelties as understood here. Wright's shifting balance theory gives conditions (e.g. population structure) under which new variation is more likely to arise and persist but does not provide a mechanistic account of how genotypic changes generate qualitatively distinct phenotypic variation through developmental pathways at particular phylogenetic junctures.[189]

5.5.2. Comparative Development/Epigenetics, Morphology, and Paleontology

Comparative embryology, morphology, and paleontology are the traditional homes for investigations of the origin of evolutionary innovation and novelty (Chapter 4). Several examples from more recent work in these domains are reviewed in the following sections.

5.5.2.1. Comparative Development/Epigenetics

Two basic domains can be identified for non-genetic approaches to explaining evolutionary innovation and novelty in developmental studies: comparative development and epigenetics. The former shares many similarities with comparative embryology while the latter emphasizes the role of non-genetic interactions during ontogeny that might be responsible for the

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[189] Although Wright's *explanandum* was different, he was sensitive to the significance of epistasis among genes during ontogeny in the production of phenotypic characters (in contrast to Fisher). It is critical to remember that epistasis among alleles *on fitness* is not equivalent to epistatic effects among genes *during development*.

production of novel morphology. In modern comparative development (e.g. comparing mesoderm formation across different taxa) there remains a concern with the ‘origin of higher taxa’ (e.g. Hanken 1986) and phylogenetic questions (Lüter 2000). Much of the research is centered on heterochrony (change in developmental rate or timing) with respect to size, shape, initiation of developmental pathways, and changes in the ordering or nature event sequences in ontogeny (Alberch 1985; Alberch *et al.* 1979; Gould 1977, 1992; Jeffery *et al.* 2002; McKinney 1988; McKinney and McNamara 1991; McNamara 1990, 1995, 1997; Raff and Wray 1989; Smith 2001, 2002; Zelditch, Sheets and Fink 2000; Zelditch and Fink 1996).

Heterochrony in salamander lineages can truncate overall development and lead to miniaturization, thereby producing novel head and forelimb morphologies, sometimes independent of specialization required in locomotion, feeding, or ecological fit (Alberch and Alberch 1981; Hanken 1984, 1985; Hanken and Wake 1993; Larson *et al.* 1981; Roth and Wake 1989; Wake and Larson 1987; Wake and Roth 1989). A famous case of heterochrony is the origin of the Mexican axolotl via paedomorphosis (Voss and Shaffer 1997; Voss *et al.* 2000). Anuran direct development involves the truncation of many developmental events and an overall more rapid embryogenesis with multiple novel features (Callery, Fang and Elinson 2001; Elinson 2001; Hanken, Jennings and Olsson 1997), something also observed in echinoids (Section 5.4) and salamanders (Wake and Hanken 1996). Major changes between sister-species can be induced with a change in a single parameter of developmental timing for the onset of particular ontogenetic trajectories (Holtmeier 2001). The study of the origin and evolution of larval forms is a key domain for comparative development investigations of innovations and novelties (Hall and Wake 1999). Human evolution and the various innovations and novelties of our lineage (e.g.

bipedalism or brain size and structure) have been another locus for studies of heterochrony (Minugh-Purvis and McNamara 2002; Verhulst 2003).

Turning to epigenetics, it is first important to clarify the meaning intended by proponents utilizing it to explain innovations and novelties.

> In using the term "epigenetic", developmental biologists wish to emphasize the context-dependence of developmental processes, geneticists refer to mechanisms of gene regulation that do not required change of DNA sequence, evolutionary biologists imply non-DNA-based mechanisms of inheritance, and population geneticists evoke phenotypic variation in response to environmental conditions" (Müller and Olsson 2003, 114).

The 'developmental biology' use is relevant here with an emphasis on non-genetic aspects of the developmental context: all factors that act on the material of the zygote through to a mature adult organism, including but not limited to those having a genetic basis that are necessary to generate every feature of multidimensional morphology present (cf. Løvtrup 1974; Müller and Newman 2003b; Schlichting and Pigliucci 1998, ch. 8). Some of these include maternally inherited cell membranes, self-organizational properties of cell and tissue interactions, spatial location of material components, physical properties of extracellular products, tissues, or cellular constituents, and biomechanical properties of growing tissues. Cells grown in a two-dimensional layer behave differently than those grown in a three-dimensional matrix (Bissell *et al.* 2003). Fibronectin is recurrently involved in branching morphogenesis during organ formation (Sakai, Larsen and Yamada 2003). Embryonic motility stimulates the formation of cartilaginous and skeletal elements (Müller 2003a). Mechanical compression of cells and tissues, such as in fluid forces operating in heart development (Hove *et al.* 2003) and the establishment of left/right asymmetry (Nonaka *et al.* 2002), induces altered gene regulation (cf. Tschumperlin *et al.* 2004; Wang *et al.* 2005). These different epigenetic properties generate predictable morphological consequences in different developmental processes (Oster *et al.* 1988).

Focusing on the physical properties of soft, excitable matter such as cells and tissues (Newman 1994, 1998, 2003), Müller and Newman have argued that most evolutionary novelties arose due to internal and external causal factors in the environmental milieu of developing organisms at an early point in evolutionary history without being genetically specified (Newman 1994; Newman and Müller 2000). Genetic specification evolves subsequently to 'hardwire' these phenotypes. Evolutionary novelties of more recent origin also may have begun as epigenetic byproducts of tissue and organ interactions via threshold effects, maintenance of transitory structures, or the switching of developmental mechanisms (cartilage formation versus bone formation) (Müller 1990, 1991a; Müller and Streicher 1989).

Another epigenetic property of developmental systems, self-organization, has also been invoked to explain the origin of novelties. Interactions that are a function of cell-adhesion lead to self-organizing outcomes in developmental processes (Steinberg 2003) and spontaneous symmetry breaking produces the polarized structures of actin comet tails (Kirschner, Gerhart and Mitchison 2000). Kauffman has argued that the self-organizational properties of developmental regulatory gene networks produce particular stable configurations in organismal structure and function (Kauffman 1993; cf. Kitano 2004; Striedter 1998, 1999).

5.5.2.2. (Functional) Morphology

Morphological (or comparative anatomy) investigations of the origin of evolutionary innovations and novelties have already been observed in Chapter 4 (Bock 1959) and the origin of novelty is often referred to as *the* 'morphological problem' (Thomson 1992). Contemporary examples include the origin of bilaterians (Dewel 2000), internal fertilization (Buckland-Nicks and Scheltema 1995), accessory pulsatile organs ("auxiliary hearts") in insects (Pass 2000), moveable abdominal lobes in male sepsid flies (Eberhard 2001), arthropod segmentation (Budd 2001b), upper jaw protrusion mechanisms in sharks, skates, and rays (Wilga *et al.* 2001), endothermy in specific groups of teleost fishes (Block 1991), feeding mechanisms in loricarioid catfishes (Schaefer and Lauder 1986), amphibian feeding mechanisms (Reilly 1994; Roth and Wake 1989; Schwenk and Wake 1993; Wake and Larson 1987), the posture stabilizing role of epaxial muscle activity in amniote locomotion (O'Reilly, Summers and Ritter 2000; Ritter 1995), carpal and tarsal elements (i.e. mesopodia) of salamander limbs (Shubin and Wake 1996; Shubin, Wake and Crawford 1995), reptilian yolk sac placentation (Stewart 1993; Stewart and Thompson 1996), biting/tearing off feeding behavior in snakes (Jayne, Voris and Ng 2002), the tapir proboscis (Witmer, Sampson and Solounias 1999), and running locomotion in vampire bats (Riskin and Hermanson 2005). The studies usually concentrate on a particular set of anatomical features in multiple taxa, such as reproductive anatomy of different marsupial and placental mammals in the study of eutherian mammal origins (Lillegraven *et al.* 1987).

Many of these studies do not sharply distinguish evolutionary innovation and novelty from key innovations (see Chapter 2). One of the most famous examples is the origin of the pharyngeal jaw apparatus in cichlid fish, which allowed a massive proliferation of species in African lake habitats by differential specialization of feeding structures (Liem 1973, 1980, 1990; cf. Galis and Drucker 1996; Jensen 1990; Rüber and Adams 2001; Streelman *et al.* 2003). The morphological reorganization within the pharyngeal jaw apparatus brought about by the presence of two new joints, a sutured connection, and a shift of insertion points for two muscles made it possible for cichlids to adopt a wide range of feeding specializations with amazing efficiency in adaptive zones with different diet opportunities. The origin of this new morphological complex is dissected by attending to the ontogenetic trajectories of its components, providing a possible mechanism whereby “relatively simple genetic alterations could slightly affect the scheduling or velocity of ontogenetic events, which in turn are capable of producing adult phenotypic changes of rather profound but not monstrous dimensions” (Liem 1973, 439).

A few themes in these studies deserve comment. First, asymmetry in studies of form and function continues to be evident but with a new twist, observable in a feeding innovation of crab-eating snakes (Jayne, Voris and Ng 2002). No structural modification was necessary for this unique bite-tear behavior to originate in a homalopsine snake species, which allows it to consume large and unwieldy prey (e.g. crabs) that cannot be swallowed. Thus, although functions are usually composed of multiple form units (many → one; Chapter 3), they may also be composed of multiple function units unidentifiable apart from endocrinological or behavioral studies. The study of elasmobranch upper jaw protrusions found novel muscle activity in addition to structural modifications, such as the origin of new muscle (Wilga *et al.* 2001).

A second theme is that these studies are often much more conscious of the interconnections between the characters under study and other features of the organism. In order to understand the origin of a particular feature, attention must be devoted simultaneously to a variety of *other* forms, functions, and their interactions, including cartilaginous elements, innervations, blood vessels, and organs involved in functions such as feeding, locomotion, and respiration (cf. Budd 2001b; Pass 2000; Witmer, Sampson and Solounias 1999). One consequence is the recognition of compositional and procedural hierarchies in evolutionary time, as seen in the seventeen changes (from new muscle insertion points to new cartilaginous elements) underlying a novel loricarioid catfish feeding mechanism (Schaefer and Lauder 1986).

Finally, these studies are very conscious of developmental patterns involved in the characters under scrutiny. For example, in the study of insect auxiliary hearts (Pass 2000), an evaluation of relevant functional demands indicates that the morphological diversity of these organs is a consequence of their source of co-option (whether from developmental precursors found in the wing, central body cavity, legs, or antennae) and is not tied to their physiological performance. Some of the studies require an analysis of reproduction, as in the case of reptilian placentation (Stewart 1993; Stewart and Thompson 1996), whereas others recognize the significance of developmental processes for the evolution of morphological features (Budd 2001b; Shubin and Wake 1996; Shubin, Wake and Crawford 1995). A few studies have been controversial because of their purported implications for the role of development in evolution (e.g. Eberhard 2001, 2002; Wagner and Müller 2002). The research on amphibian feeding and cranial morphology innovations and novelties explicitly invokes heterochrony and developmental reprogramming to explain morphological change (Hanken 1984, 1985; Hanken and Wake 1993; Liem and Wake 1985; Reilly 1994; Roth and Wake 1989; Wake and Hanken 1996; Wake and Larson 1987).

The identification of these aspects of morphological research on innovations and novelties is not simply a result of my literature survey. Morphologists have been methodologically reflective about their concepts and practices (Dullemeijer 1974, 1981; Hickman 1991; Lauder 1990, 1991; Liem and Wake 1985; Schwenk 2001), and aware of the interdisciplinary prerequisites for much of their research (Galis 1996; Liem and Wake 1985; Wake 1992). They have been willing to embrace molecular techniques when appropriate (Block 1991; Larson *et al.* 1981), develop their own experimental tools such as electromyography (Gans 1985; Hanken and Wake 1991), and are self-conscious about the use of a phylogenetic context for their research (Lauder 1981, 1982, 1990; Lauder *et al.* 1995; Wake 1992). They have been wary of inferences from structure to function (and *vice versa*) (Dullemeijer 1974, 1981; Gillis and Biewener 2003; Lauder 1990, 1995), one of the reasons they attend to the interconnections among forms and functions in character complexes (Galis 1996; Schwenk 2001; Schwenk and Wagner 2001), and are attuned to the ontogenetic aspects of their research (Galis 1996; Liem and Wake 1985; Thomson 1988, 1992; Wake 1992). Reflections on the nature and significance of experimental data, the testing of hypotheses, and building of models have also received attention (Fisher 1985; Homberger 1988; Lombard 1991). This methodological reflection is also a feature of paleobiological research (Alexander 1989, 2003; Budd in preparation; Plotnick and Baumiller 2000), which is natural given its multiple points of contact with morphological research.[190]

5.5.2.3. Paleontology (and Paleoecology)

Paleontological investigation naturally coordinates with morphological studies. Research has focused on a variety of 'difficult' evolutionary transitions but the origin of tetrapod limbs (and paired appendages) has been a perennial favorite (Coates 2003; Shubin 1995; Vorobyeva and Hinchliffe 1996). Explanations of tetrapod limb origins have been transformed in the past fifteen years with the discovery of a variety of new fossil forms, including a diversity of new taxa (Clack 2002a; Clément *et al.* 2004; Paton, Smithson and Clack 1999; Shubin, Daeschler and Coates 2004; Zhu, Ahlberg and Zhao 2002; Zhu and Yu 2002; cf. Clack 2002b). The earliest tetrapods were aquatic (Clack *et al.* 2003; Coates and Clack 1990, 1991; Shubin, Daeschler and Coates 2004) and had polydactylous limbs (>5 digits) (Coates and Clack 1990), with pentadactyly obtained secondarily in terrestrial taxa (Clack 2002a; Paton, Smithson and Clack 1999; cf. Clack 2002b). This digital reduction trend was interpreted within ontogenetic models

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[190] An analysis of the details of this methodological reflection would take us too far a field from the main discussion. This brief overview highlights that some of the issues identified in my analysis (such as the significance of interconnections among forms and functions in character complexes) have also been discussed by morphological and paleontologial researchers.

of limb and digit development (Coates 1991; Coates and Clack 1990; Hinchliffe 1989; Shubin and Alberch 1986), as well as emerging knowledge of molecular developmental genetics of the tetrapod limb (Coates 1991). Paleontological researchers have collaborated with developmental researchers to generate hypotheses and execute research on the origin of paired appendages and the tetrapod limb (Coates 1994; Coates and Cohn 1999; Grandel 2003; Hinchliffe 1989, 1994; Shubin, Tabin and Carroll 1997; Shubin 2002; Vorobyeva and Hinchliffe 1996). These studies make direct contact with those focusing on developmental genetics (cf. Section 5.2.1) and have been primarily concerned with correlating paleontogical *patterns* in morphology with developmental genetic research related to the ontogenetic *processes* producing the morphology.

Similar kinds of studies are identifiable for other taxonomic groups. Some of these include the origin of ligamentary invagination in rudist bivalves (Skelton 1985), dorsal ridge scale patterning in semionotid fishes (McCune 1990), the origin of internal nostrils in tetrapods (Zhu and Ahlberg 2004), the origin of the wooly mammoth (Lister and Sher 2001), and the origin of mammals (Kemp 1982, 1985). Two components of the paired fins/tetrapod limb example and these other studies stand out. First, there is a natural conceptual 'reach'[191] for developmental data to interpret the origin of the variation for a particular transition. This is quite explicit in a recent study on internal nostrils in tetrapods.

> It is striking that the development of the nasal region in tetrapods seems in some ways to recapitulate the evolutionary transformation illustrated by *Kenichthys*. … Failure of this process [fusion of central and maxillary prominences in humans] results in a cleft lip, mirroring the gap between the premaxilla and maxilla in *Kenichthys*. This joining of the central and maxillary prominences resembles a recapitulation of the re-establishment of maxillary-premaxillary contact at the *Kenichthys*-rhizodont internode. The occurrence of cleft lip and palate are know to be associated with failure of *Bmp* and/or *Shh* + *ptc* expression, regulating the growth of the central and maxillary prominences as well as the epithelial breakdown that allows them to fuse, which indicates that the components of

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[191] This is the terminology used by Michael Coates to describe his own research strategy during a conversation with the author at the University of Chicago in May 2003.

> this pathway might have been involved in regulating the evolution of the choana (Zhu and Ahlberg 2004, 96).

These studies also indicate continuity in language with those studied in Chapter 4, where the origin of higher taxa and the origin of innovations and novelties were coupled. Paleontologists still move back and forth between these two designations.

One particular strategy for explaining evolutionary innovations and novelties observable in paleontological research is the appeal to particular abiotic or biotic environmental conditions. Vrba attempts to correlate particular environmental conditions during geological periods with 'explosive' evolutionary change on the assumption that global environmental change must be responsible when *multiple* lineages respond in a concentrated geological time slice (Vrba 2004). The Cambrian explosion (~540mya) is connected with fluctuations in global climate (including a warming epoch) (cf. Vermeij 1995), enhanced phytoplankton productivity (cf. Butterfield 1997), rise in oxygen concentration in atmosphere and ocean, and availability of biomineralization materials for hard skeleton formation (cf. Erwin 1993; Knoll and Carroll 1999; Valentine 2004). The late Carboniferous (~300mya) saw the first major radiation of flying insects, major increases in aquatic invertebrate size, and land vertebrate diversification, which are all connected to the rise of atmospheric oxygen and decline in carbon dioxide concentration. The Late Neogene (past several million years) has seen a general cooling trend in global temperatures (including ice ages), which may have aided the radiation of African mammals with body enlargement across most taxa. Vrba hypothesizes that global cooling induces the prolongation of growth (a type of heterochrony), which leads to various morphological changes including size increase. Although these are *correlations*, features of the altered environment can be cited with respect to specific characters, such as greater density of a hyperoxic atmosphere allowing small incipient wing structures to generate lift and elevated oxygen enhancing primitive terrestrial lung effectiveness in the late Carboniferous. In addition to these abiotic factors, others have emphasized biotic interactions. Vermeij argues that predator-prey interactions have been an engine of morphological diversification leading to species with inherently higher versatility to produce different protective or predative morphology, especially among marine invertebrates (Vermeij 1973, 1987, 1994, 2001; but see Masters and Rayner 1993).

Jablonski and others have identified several paleoecological correlations for the origin of evolutionary novelties in marine invertebrates, including the tropics as a favored biogeographical locale (Jablonski 1993). Different bryozoan groups do not show distinct patterns of novelty origin based on onshore versus offshore ecological settings, but have differing rates of novelty origin at distinct phylogenetic junctures (Jablonski, Lidgard and Taylor 1997). This is in contrast to novelties arising in taxa in the early Paleozoic (e.g. Cambrian-Ordovician), where an onshore origination bias is distinguishable (Jablonski and Bottjer 1990; Jablonski and Bottjer 1990; Jablonski and Bottjer 1991; Jablonski *et al.* 1983).[192] Potential reasons for this include those already cited, low-diversity in particular onshore niches (Erwin, Valentine and Sepkoski 1987), and ecologically triggered heterochrony due to unstable environments (McKinney 1986; cf. Jablonski and Bottjer 1990; Valentine 2004).[193] Symbiotic processes have also been invoked for the origin of novelties (McKinney, Broadhead and Gibson 1990; Norris 1996). Hoffman and Parsons have tried to generalize these kinds of explanations to extinction, diversification, and evolutionary rates: "Evolutionary novelties appear to be mainly a feature of disturbed habitats with high levels of primary productivity" (Hoffman and Parsons 1997, 204).

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[192] Others claim this pattern does not hold for the 'early' Cambrian (Mount and Signor 1985), although they operate in a similar mode when identifying shallow subtidal environments as the locus of marine invertebrate innovation.

[193] Explanations invoking low diversity (or 'open niches') receive further support from analyses that look at ecologically open guilds after mass extinctions (Ciampaglio 2004).

In most of these explanations the problem agenda of innovation and novelty ('origination') and the problem agenda of adaptation ('radiation', diversification, or key innovation) are not cleanly separated, especially when paleoecology is being considered (Hunter 1998; Hunter and Jernvall 1995). But this does not prevent researchers from attending to the developmental questions underlying the origin of variation at a particular phylogenetic juncture (Jernvall 2000; Jernvall, Keränen and Thesleff 2000). Another aspect of these studies is a bias toward evolutionary novelties over innovations, which is to be expected given the fossilization of hard skeletal parts. Paleontological researchers have attempted to dissect the origin of functional features, such as bat echolocation (Fenton *et al.* 1995) or the hearing and locomotion of whales (Nummela *et al.* 2004; Spoor *et al.* 2002; Thewissen, Hussain and Arif 1994), but usually indirectly through anatomical inferences.

The final aspect is an intersection of documenting pattern and offering process explanations. Many of the above studies are elucidating particular patterns from the fossil record rather than providing an explicit causal explanation (often offering multiple possible or plausible mechanisms). Two aspects of this juxtaposition of pattern and process issue are important. First, evolutionary innovations and novelties have arisen in a nonrandom fashion with respect to space and time through the history of life (Erwin 2000). Second, documented patterns constrain causal process explanations (Jablonski and Bottjer 1990). Without these paleontological studies, patterns relevant to phylogenetic junctures under consideration for the origin of specific innovations or novelties would remain unknown. Paleontologists have recognized their inclination toward extrinsic or 'environmental' causes for the patterns they isolate (Allmon and Ross 1990), which is reflected in 'paleoecological' explanations, but they are also focused at higher levels of organization (Gould 1995, 2002; Jablonski 1986, 1987, 2000; Valentine 2004), which is especially important for studies of innovation and novelty.

Two comments are in order as we close these three related subsections. First, these disciplinary communities are still the primary loci for studying evolutionary innovations and novelties. Even though developmental genetic explanations have been receiving increased attention, the problems and experimental approaches identifiable in mid-20th century research are also present today. These parallels emerge at the level of language similarity in the use of the origin of higher taxa alongside the origin of evolutionary innovations and novelties. Second, each of these disciplines recognizes the importance of a phylogenetic context in the execution of their explanations having participated in the sea change in systematic methodology that occurred over the past three decades (Hull 1988b).

5.5.3. Behavioral Biology

Studies of innovation have not proceeded apace with investigations of evolutionary novelty. Examples of explanations of the origin of novel functions from behavioral biology are less numerous but available (cf. Reader and Laland 2003a), such as lizards determining the sex of embryos via selective temperature regulation (Robert and Thompson 2001), cooperative swarming in bacteria (Velicer and Yu 2003), running in vampire bats (Riskin and Hermanson 2005), courtship song and communication in drosophilid flies (Hoy 1990; Hoy, Hoikkala and Kaneshiro 1988), and feeding behavior in snakes (Jayne, Voris and Ng 2002, see discussion above). Many fewer have been subjected to intense scrutiny in a phylogenetic context or with respect to the mechanistic basis of the relevant variation being produced during ontogeny.[194]

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[194] Some of these were observed within functional morphology (e.g. feeding and locomotion). Throughout this section I am using innovation (noun) as a product rather than process term (cf. Reader and Laland 2003b).

The foraging and feeding behavior of fishes and birds have been one topic of investigation. Studies of foraging in guppies found that females were more likely to innovate than males, food-deprived fish were more likely to innovate than their well-fed counterparts, and smaller fish were more likely to innovate than larger fish (Laland and Reader 1999a, 1999b). Fish that had previously innovated were more likely to do so subsequently, seemingly indicating an 'innovation disposition' in certain individuals (Laland and Reader 1999a; cf. Laland and van Bergen 2003). Once extant, these behaviors based on novel information spread rapidly in populations via learning mechanisms, although more rapidly in females than males (Reader and Laland 2000). Avian feeding innovations are tightly correlated with forebrain size (Lefebvre *et al.* 1998; Lefebvre *et al.* 1997; Nicolakakis and Lefebvre 2000; cf. Lefebvre and Bolhuis 2003), specifically the hyperstriatum ventrale in the dorsal ventricular ridge (Timmermans *et al.* 2000). This behavioral flexibility confers an advantage on certain avian groups to invade new environments (Sol and Lefebvre 2000), including the ability to feed near novel objects (Greenburg 2003; Webster and Lefebvre 2001). The connection between behavioral innovation and forebrain size also holds in primates, where chimpanzee males of lower social rank exhibit the greatest propensity to innovate foraging behavior, as well as in social interactions (Boesch 1995; Reader and Laland 2001; Reader and Laland 2002). These behaviors can be faithfully transmitted to future generations.

Studies of behavioral innovation tap into a larger theme regarding the role of behavior in evolutionary change (Baldwin 1897; Lloyd Morgan 1896, 1933), especially whether it leads ('nurture'; Hunt and Gray 2003) or follows ('nature'; Kenward *et al.* 2005) in the evolutionary process. Farmer has argued that parental care is the underlying cause for endothermy (evolutionary innovation) in birds and mammals (Farmer 2000, 2003). Although controversial

(Angilletta and Sears 2003), it shows the use of behavior as a cause (or *explanans*) in explanations of the origin of innovations. A number of biological researchers have attempted to articulate research programs that highlight a causal role for evolutionary change through attention to the ontogeny of behavior (e.g. Bateson 2001; Gottlieb 1992, 2001, 2003). Discussions have revolved around ideas such as the 'Baldwin effect' (organic selection), genetic assimilation, and niche construction, *inter alia* (Ancel 1999; Arnold 1992; Bateson and Martin 1999; Budd 1999; Hall 2001; Laland, Odling-Smee and Feldman 2001; Odling-Smee, Laland and Feldman 1996; Oyama, Griffiths and Gray 2001; Simpson. 1953; Sterelny 2001; Waddington 1942; Weber and Depew 2003; Wilkins 2003). Although none of the explanations of behavioral innovations utilize developmental genetics, there is a healthy discussion about the status of gene-based explanations of behavior and the role of ontogeny and environment (Bateson 1983, 1998; Bateson and Martin 1999; Gordon 2001; Rose 1998; Schaffner 1998a), as well as studies of gene network interactions in the production of simple behaviors (e.g. van Swinderen and Greenspan 2005).

5.5.4. Ecology (and Environment)

Ecology and environmental approaches to the origin of evolutionary innovations and novelties coordinate with behavioral approaches, as many discussions regarding the significance of behavioral ontogeny for evolution concern altered environmental factors (e.g. Hall 2001; Hall, Pearson and Müller 2004; West-Eberhard 2003). In Waddington's genetic assimilation (Waddington 1942), some environmental stimulus affects ontogeny such that a morphological (or behavioral) outcome emerges that benefits an organism. This ontogenetic difference is subsequently incorporated into the genetic constitution of the species and therefore propagated to descendants. There has been less attention to extant ecological factors in the origin of innovations and novelties because the phylogenetic juncture demands a *paleo*ecological mode.

Following the distinction between biotic and abiotic ecological factors, biotic factors have been studied in a few cases; competition among terrestrial gastropods reduced species representation in vitrinid semislugs but areas without direct competition from slugs allowed for increased speciation via the origin of limacization ('becoming a slug') in vitrinid semislugs (Hausdorf 2001). Coevolutionary studies have repeatedly confirmed that 'arms races' occur between particular pairs of species (Gomulkiewicz *et al.* 2000; Nuismer, Thompson and Gomulkiewicz 1999, 2000; Thompson 1994, 1997, 1998, 1999a, 1999b, 1999c; Thompson and Cunningham 2002; Vermeij 1994), which can in principle lead to rapid morphological diversification. This includes host-parasite interactions (Bermudes and Joiner 1993; Forde, Thompson and Bohannan 2004). The difficulty with these explanations is that they explain why variation will be selected but not how it originated. Ecologically oriented studies that make contact with the origin of variation are found under the heading of *phenotypic plasticity*.

Phenotypic plasticity is the capacity of an organism with a particular genotype to produce more than one phenotype under different environmental regimes (Gordon 1992; Pigliucci 2001a, 2001b; Scheiner 1993; Schlichting and Pigliucci 1998), including in the exploratory behavior of biological systems during ontogeny, such as the plasticity found in the developing nervous system (Gerhart and Kirschner 1997, ch. 4). The range or extent of this capacity is referred to as a *norm of reaction* (Schlichting and Pigliucci 1998), which may or may not be explicitly adaptive (Sarkar 1999; Travis 1994).[195] Examples include the heights of plants in soils of differing nutrient content or the developmental plasticity in jaw size of snakes encountering different sized prey (Aubret, Shine and Bonnet 2004). Environmental factors, biotic or abiotic, can dramatically

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[195] Norms of reaction can be generalized for plasticity at and above the population level (Sarkar and Fuller 2003).

impact the development of adult morphology (Pigliucci 2001b; Sarkar 1999; Schlichting and Pigliucci 1998; Van der Weele 1999). In frog tadpoles, predator presence in the larval environment accelerates the advent of metamorphosis (Relyea 2000; Relyea and Werner 1999, 2000), which is a part of an adaptive developmental norm of reaction to heterogeneous environments (Van Buskirk and Relyea 1998; Van Buskirk and Saxer 2001). Morphometric correlations in tiger salamander skull features suggest that life history variations arose through heterochrony favored by intraspecific competition (Collins, Zerba and Sredl 1994).

Abiotic factors also alter ontogenetic trajectories, sometimes in the form of teratologies (Gilbert 2001). Variation in the amount of exogenous thyroid hormone acquired from an algal diet in echinoids has been implicated in the transition from indirect to direct development, in part because thyroid hormone induces metamorphosis (Heyland and Hodin 2004; Heyland, Hodin and Reitzel 2004; Heyland, Reitzel and Hodin 2004). Some undersea vent worms undergo developmental arrest until they encounter appropriately warm temperatures (Pradillon *et al.* 2001) and soil nematodes respond similarly to stressful conditions with a 'dauer' larval stage (Gerisch *et al.* 2001; Wang and Kim 2003). Stressful environments can induce developmental variability, such as greater fluctuating asymmetry (Hoffman and Parsons 1991, 1997; Hoffman and Schiffer 1998; Parsons 1994), which can then be genetically stabilized to generate evolutionary change (Zakharov 1994). Differences in feeding during development can affect morphological outcomes through heterochrony (Meyer 1987) or by generation of completely different morphs (Greene 1989, 1996). Some of these differences can be traced to the mediating effect of hormones (Dufty, Clobert and Møller 2002).

The primary explanatory argument for the role of phenotypic plasticity in the origin of innovations and novelties comes from West-Eberhard (West-Eberhard 1989, 2003; cf. Pigliucci

2001a, 378-381; 2001b, ch. 9; Schlichting and Pigliucci 1998, 316ff). Environmentally induced features (especially behavior) that are a ‘hidden’ or ‘rare’ part of a reaction norm and benefit an organism will be subsequently stabilized genetically under favorable environmental conditions. This mechanism operates on multiple features simultaneously since the environmental induction impinges on the developmental trajectories of several characters. The existence of qualitative differences in phenotypes of populations (‘alternative phenotypes’ or polyphenisms) means that morphological change via developmental change can occur within a particular lineage, which only later diverge into two distinct species (cf. Balon 2004; Sinervo and Svensson 2004). Behavioral imprecision of web building in certain spider taxa has led to a high diversity of web designs (Eberhard 2000).

This proposal is conceptually akin to earlier thinking on genetic assimilation (Waddington 1942), ‘stabilizing selection’ (Schmalhausen 1986 [1949]), and the Baldwin effect (Baldwin 1897; Hall 2001; Weber and Depew 2003). A previously noted difficulty that arises for this explanatory strategy is the demonstration that novel variation origin is possible but (in most cases) does not explain the origin of variation at particular phylogenetic junctures. When phylogenetically situated, these studies can be persuasive, such as developmental plasticity due to feeding differences in the evolution of species of fish (Day, Pritchard and Schluter 1994; Meyer 1987), or the role of hormones in the origin of insect morphology (Abouheif 2004; Moczek 2003; Moczek and Nijhout 2002, 2003) and life history transitions in echinoids (Heyland and Hodin 2004; Heyland, Hodin and Reitzel 2004; Heyland, Reitzel and Hodin 2004).

Recognizing explanations of innovation and novelty that appeal to the environment or ecology is critical because the potential effects of these factors are minimized in laboratory systems used by developmental geneticists (Gilbert 2001). Several of the disciplinary domains reviewed converge in their explanatory strategies. External environmental factors (‘ecology/environment’) such as temperature and light conditions affect embryonic motility (‘behavior’) in chick embryos. The degree of movement executed (‘behavior’) has an effect on the induction of cartilage and bone formation through mechanosensitive stimulation (‘epigenesis’), including the formation of *de novo* skeletal elements (Müller 2003a; cf. Hall, Pearson and Müller 2004). Intraembryonic movement can also be studied from the perspective of functional morphology.[196]

5.5.5. Molecular Biology and Genetics

The rise of molecular biology (cf. Morange 1998) and the treatment of innovation and novelty at lower levels of organization is one of the major changes in attempted explanations of innovation and novelty over the past four decades. These studies have added a new cache of forms and functions that originated at particular phylogenetic junctures in the history of life that stand in need of explanation. Explanations at the molecular biological level require different resources because causes invoked to explain the origin of higher-level innovations and novelties, such as changes in developmental genetic expression via gene duplication, become the *explanandum* (how does gene duplication occur?). The origin of new genes (form = novelty) is a natural point of entry (Long *et al.* 2003b). A number of mechanisms can generate new genes: gene fusion, tandem duplication, unequal crossover during meiosis (illegitimate recombination), incorporation of supernumerary chromosomes, polysomy, polyploidy, retrotransposition, lysogeny (incorporation of viral genes), inter-organelle transfer after symbiosis, and horizontal transfer (Long *et al.* 2003a; Long *et al.* 2003b; Ochman, Lawrence and Groisman 2000; Ohno

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[196] This convergence of disciplinary approaches is not the same as an active integration of explanations (see Chapter 6). Rather, it highlights ‘natural’ connections among the different disciplines (see below, Section 5.6).

1970, Part 4; Stibitz, Keeling and Bhattacharya 2000; Zuckerkandl 1975). The origin of form (novelty) and function (innovation) are tightly coupled in most of these investigations. New gene functions often arise through exon shuffling (either due to a retrotransposed exon or illegitimate recombination) from existing genes and retrotransposition (Long *et al.* 2003a; Long *et al.* 2003b; Patthy 2003).

For example, the *Drosophila* gene *Jingwei* arose through chimeric fusion due to exon shuffling of *alcohol dehydrogenase* and a duplicate copy of the gene *yellow emperor* (Wang *et al.* 2000). A similar process was involved in the origin of the *Drosophila* gene *sphinx* (Wang *et al.* 2002; cf. Wang, Yu and Long 2004). A paternal effect gene essential for zygote viability in *Drosophila* originated through retrotranspositional duplication and neofunctionalization via transcriptional coregulation to male germ-line specific regulation (i.e. it adopted the expression profile shared by the gene flanking the duplicate) (Loppin *et al.* 2005). The origin of vertebrate steroid receptors has been explained by ligand exploitation, a process whereby duplicate receptors resulting from genome expansions capture different steroid pathway components in addition to the end product (Thornton 2001; cf. Crews, Willingham and Skipper 2000).

Cellular organelles have also come under scrutiny with respect to their evolutionary origination. One popular explanation is symbiosis between two distinct species (Dyall, Brown and Johnson 2004; Margulis and Fester 1991; cf. Sterelny 2004). The origin of hydrogenosomes (anaerobic function) has been explained via anaerobic modifications of mitochondria (aerobic function), especially massive gene loss, after an initial endosymbiotic event or by specialization of a facultative anaerobic/aerobic endosymbiont (Boxma *et al.* 2005; Dyall *et al.* 2004; Embley *et al.* 2003; Hrdy *et al.* 2004). Similar explanation types exist for mitochondrial origins (Andersson *et al.* 2003; Gray, Burger and Lang 1999).

Innovations at the molecular biological level also require explanation. How did alternative splicing of mRNA originate (Ast 2004)? This requires attention to the origin of introns in eukaryotic genes (e.g. Qiu, Schisler and Stoltzfus 2004), a procedural hierarchy in evolutionary time. One explanation is that constitutive splicing degenerated into alternative splicing through sub-optimization of splice site binding via mutation accumulation, allowing for exon skipping (Ast 2004). Another explanation focuses on tandem exon duplication (Kondrashov and Koonin 2001). Similar questions can be asked of DNA replication and repair, transcriptional and translational functions, cytoskeletal transport of proteins, mitosis and meiosis, and others. Biochemical pathways constitute another group of innovations. Different aerobic and anaerobic metabolic pathways appear to have arisen out of a combination of preexisting biochemical pathways (Dismukes *et al.* 2001; Livingstone 1991).

The critical feature of these different explanations of molecular biological innovations and novelties is that development is much less important. This is largely because much of the hierarchical structure constructed during ontogeny is not in focus. Even in those molecular studies most sensitive to issues of genotype-phenotype mapping concerning secondary structure in RNA (discussed in Chapter 2), there is an explicit recognition of differences.[197] The difficulty becomes quite explicit when the origin of multicellularity is under investigation. It is not clear whether multi-level selection theory, molecular and cell biology, or comparative morphology should be adopted as the appropriate explanatory framework (Aravind and Subramanian 1999; Bonner 2000; Buss 1987; Dewel 2000; Maynard Smith and Szathmáry 1995; Michod 1999).

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[197] "The RNA model is not a representation of organismal development. The regulatory networks of gene expression and signal transduction that coordinate the spatiotemporal unfolding of complex molecular processes in organismal development … have no concrete analogue in the RNA sequence-to-structure map. Developmental processes themselves evolve and this too is outside the scope of the rather simple notion of RNA folding considered here" (Fontana 2002, 1164).

5.6. Thematic Observations and Preparation for Analysis

This chapter has involved the review of a large amount of biological detail. Some of this will be exploited in Chapter 6 when we reconstruct conceptual clusters for different approaches to explaining evolutionary innovations and novelties. Several themes emerge by viewing these approaches side by side. One is coincident with our results from Chapter 4—the bias toward explaining novelties rather than innovations. (Only in behavioral biology investigations is this bias reversed.) Another is that evolutionary genetics has an antagonistic relationship with studies of evolutionary innovation and novelty. There is resistance to accepting evolutionary innovations and novelties as distinct phenomena (the presupposition of the problem agenda of innovation and novelty) and population genetic methodology is ill suited to address their origin. Because of the central role of evolutionary genetics in a neo-Darwinian evolutionary perspective, the exclusion of research on evolutionary innovations and novelties receives a partial explanation in virtue of this resistance. Accusations of typological thinking intercalate with conceptualizing the origin of novelties as a question concerning the gradual transition from one phenotype to another (cf. Amundson 1998; Love 2003a; Mayr 1959; Richardson, Minelli and Coates 1999).

We observed strong continuity with our historical analysis in comparative development/epigenetics, functional morphology, and paleontology as key foci for investigations of evolutionary innovation and novelty. This continuity includes the retention of a linguistic convention that slides back and forth between 'the origin of higher taxa' and 'the origin of evolutionary novelty'. There is also not a clean separation between origination (innovation and novelty) and diversification (key innovation). Epigenetic studies remain of interest to understanding the origin of evolutionary novelties, especially at higher levels of organization (similar to Berrill's position) although developmental genetic investigations of ontogeny dwarf them in sheer volume. Functional morphologists are self-conscious about their methodology and conceptual biases, understanding asymmetries in the study of form and function, the importance of interconnections among form and function features, and the need to consider developmental trajectories. All three of these research domains share this latter component and retain a phylogenetic focus in the sense of being explicit about a phylogenetic context, which is not as readily observable in other disciplinary approaches. This means that the origin of variation at particular phylogenetic junctures is in view, as opposed to variation *in general* as seen in other studies of gene regulation and some phenotypic plasticity investigations.

Developmental genetic research generates a plethora of data but this material is not necessarily linked into a cohesive narrative of change as is done in other disciplinary approaches. The compatibility of duplication and co-option type explanations and the necessity of multiple gene expression differences in pathways or networks likely contribute to this neglect. Less attention has been paid to the various difficulties that arise in establishing the pattern-based component. Circularity creeps in when *similarities* in gene expression alone are used to establish homology and then simultaneously deployed to explain *differences* relevant to the process of the origin of a novel feature. The echinoid ectoderm territory comparisons illuminated both difficulties involved in the process component and the advantages of combining regulatory and structural gene expression patterns with morphological features to establish non-homology.

Environmental factors are largely excluded from developmental genetic investigations because of the laboratory context and the model organisms studied are sometimes far removed from the relevant phylogenetic context for a particular innovation or novelty. A consequence of the model organism focus is sparse taxonomic sampling in developmental genetic studies in contrast to comparative development, morphology, paleontology, and other approaches (cf. Hanken 1993). This problem simultaneously allows for a large accumulation of data, as seen in the studies of craniofacial ontogeny. Investigations of arthropod novelties have been biased toward insects, whereas the tetrapod limb is primarily dissected via the chick limb bud. Developmental genetic researchers tend to view their methodological focus in causal terms, attributing gene expression changes the primary role in the origin of innovations and novelties even though there is a disparity between the hierarchical level of these innovations and novelties and the gene expression patterns investigated.

Natural connections exist among many of the disciplinary approaches. The most obvious has already been dwelt upon (paleontology-morphology-comparative development) but there are others. For example, behavior-phenotypic plasticity-epigenetics-functional morphology is also a frequent juxtaposition, as is paleontology-ecology/environment. These groupings suggest certain procedural interrelations in the investigation and explanation of evolutionary innovations and novelties, some of which have been occluded because of our exclusion of systematics from the discussion. Procedural relations among disciplines operate in tandem with the procedural relations between the pattern and process aspects of explanations of innovations and novelties. The nature of these procedural connections will be explored more fully in the next chapter.

Other disciplinary approaches to explaining evolutionary innovation and novelty are available. I have excluded discussion of physiological innovations and novelties (cf. Burggren and Bemis 1990). Phenomena from this domain include the origin of water pressure sensation in crocodiles (Soares 2002) and a 40% increase in cardiac muscle mass in pythons after feeding (Andersen *et al.* 2005). Each disciplinary approach to explaining evolutionary innovation and novelty has not been treated at the same level of detail as developmental genetic strategies. This partly reflects existing biases in the literature but also correlates with the interests of Evo-devo researchers. Although principles such as modularity are certainly transferable to the origin of genes or protein structures (Khosla and Harbury 2001; Patthy 2003; cf. Ganfornina and Sánchez 1999), these phenomena are not the primary *explananda* of Evo-devo researchers.

Before summarizing our discussion it is necessary to highlight the use of 'disciplines' or 'disciplinary approaches' as organizing units. We have already seen that the boundaries between the disciplinary units demarcated are blurry at times and that particular methodologies do not fit neatly into one or another of these research communities. And yet something is captured by this grouping that is not an artifact. It tracks the sociological, technological, and intellectual structuring of these areas of research (Bechtel 1986a, 1993; Lenoir 1997; Klein 1990; Kline 1995, ch. 15; Kockelmans 1979b; Messer-Davidow, Shumway and Sylvan 1993; Swoboda 1979). The differences in explanations offered for evolutionary innovations and novelties begin to isolate styles of reasoning (Crombie 1994; Davidson 1996; Hacking 2002b; Harwood 1993) that group disciplines into cohorts or natural alliances (Klein 1990, ch. 5), one of which was identified historically in Chapter 4 (comparative embryology, morphology, and paleontology) whereas several more emerged in this chapter. These affinities are discussed in the next chapter in relation to philosophical distinctions about explanatory types in biology and differences in conceptual cluster behavior. Although disciplinary analysis is not an exhaustive methodology for understanding scientific reasoning, it illuminates the cognitive practice of biologists.

5.7. A Short Summary

In the service of brevity, we can summarize the chapter in 'bullet-point' format.

- Developmental genetic explanations of evolutionary novelties abound in contemporary Evo-devo with studies of the role of arthropod *Hox* genes being one prominent nexus.

- The structure of developmental genetic explanations of evolutionary novelties involves both a pattern and process component that must be executed sequentially (pattern → process).
- The pattern aspect focuses on regulatory gene expression patterns across wide phylogenetic distances, which are criticized because of the dissociation between gene expression and morphology, and the use of a functional criterion of homology (shared developmental role). Structural gene expression evaluated at shorter phylogenetic distances is an alternative that does not suffer as severely from these difficulties.
- The process aspect also focuses on regulatory genes, arguing that changes in *cis*-regulatory elements of genes alter spatial (heterotopy) and temporal (heterochrony) gene expression leading to new phenotypic variation. These changes either occur for an existing gene (co-option) or utilize paralogues following duplication events (duplication), although these explanation types are not mutually exclusive. Explanations involving *cis*-regulatory changes involve multiple genes, which imply genetic pathways and networks. The modularity of these pathways/networks or larger developmental units allows explanations of evolutionary novelty to occur without consideration of all other aspects of an organism.
- Developmental genetic explanations of the origin of vertebrate jaws exhibit pattern (gill arch topology) and process (transformation of branchial arches versus velar cartilage) aspects. Phylogenetic juncture considerations concentrate on the derived nature of cyclostomes and phylogenetic relationships among extant and extinct agnathans and gnathostomes, both of which are critical in modeling the ancestral character condition from which jaws emerged.
- Many regulatory genes involved in craniofacial ontogeny, in conjunction with neural crest cells, have been studied in model organisms and lamprey species. They exhibit expression patterns and functions relevant to jaw origins from a developmental genetic perspective.

- These developmental genetic studies have introduced ambiguity and novel hypotheses into the homology judgments involved in the pattern aspect, whereas for the process aspect the multiple relevant expression patterns of regulatory genes do not yet have corresponding *cis*-regulatory element modifications to explain particular morphological changes due to gene expression alterations, either in space or time. Additional considerations from studies of pharyngeal arches, dentition, and jaw muscle may also be relevant.
- Ectoderm differentiation in closely related echinoid species differing in developmental mode provides an opportunity to observe the operational establishment of non-homology apart from fossil considerations. A review of molecular and morphological evidence along with other considerations indicates that the extravestibular ectoderm of the direct developing sea urchin *H. erythrogramma* is an evolutionary novelty.
- Seven different disciplinary perspectives were surveyed with respect to explanations of evolutionary innovations and novelties: evolutionary genetics, comparative development/epigenetics, morphology, paleontology, behavioral biology, ecology (and environment), and molecular biology/genetics.
- Population genetic models do not apply to explanations of innovations and novelties. Transitions between qualitatively different phenotypes in quantitative genetics are conceptualized in terms of phenotypic continuity rather than developmental accessibility.
- Comparative development/epigenetics, morphology, and paleontology remain key foci for studies of evolutionary innovation and novelty and retain the linguistic phraseology of earlier researchers (the origin of higher taxa ≈ the origin of innovations and novelties). Comparative development has dwelt extensively on the role of heterochrony whereas epigenetic studies highlight both the physical properties of cell and tissues and the self-organizing behavior of

developing systems. Morphology and paleontology do not cleanly separate origination (innovation and novelty) from diversification (key innovation). Functional morphologists recognize the asymmetry between studies of form versus studies of function, the necessary relevance of interconnections with other organismal parts, and developmental origin of the characters they study. Paleontological researchers also make developmental connections explicit, are biased toward form features, and favor environmental factors in explanations. Their results generate essential pattern constraints on process explanations.

- Behavioral biology focuses on organismal activities (function – innovation) but the role of behavior and its ontogeny in evolutionary explanations is contentious. Ecology and environment explanatory strategies invoke both abiotic and biotic factors, especially as they affect phenotypic plasticity. Arguments for its significance in the origin of evolutionary novelties are also contentious and tend not to be couched in a phylogenetic context (variation in general *versus* variation at particular phylogenetic junctures).
- Molecular biology introduces a large cache of new innovations and novelties (genes, organelles, alternate splicing) but explanations are fundamentally different in style (e.g. the invocation of symbioses) because developmental processes are less important. Form and function stay tightly wedded in most of these studies.
- Several general themes can be extracted. The continuity of focus in comparative development, morphology, and paleontology stems from attention to higher levels of organization, especially in terms of developmental trajectories. Owing to the predominance of evolutionary genetics in contemporary evolutionary theory, resistance to the individuation of the problem agenda of innovation and novelty can be understood as a rejection of the presupposition that the phenomena are real or distinct. Developmental genetic explanations

do not link disparate studies into a cohesive narrative of evolutionary developmental change as seen in other disciplinary approaches. They also ignore the significance of environmental factors, which are eliminated in the experimental set-up, nor is their comparative base of taxa as large as in other approaches. The experimental methodology also encourages viewing gene expression as the primary causal factor despite the hierarchical gap between gene expression and the innovations and novelties being explained.

- Natural connections exist among disciplinary approaches: (a) paleontology-morphology-comparative development; (b) behavior-phenotypic plasticity-epigenetics-functional morphology; and, (c) paleontology-ecology/environment. These groupings are related to procedural relations in explanations of innovations and novelties, such as pattern → process.

I have largely refrained from direct criticism of any particular, disciplinary approach (except in the case of evolutionary genetics). This is not to say these different putative explanations of innovation and novelty could not be criticized. Responses to some of these explanatory strategies have been quite negative and severe (e.g. de Jong and Crozier 2003). But my aim in Chapter 6 will be to focus on the shortcomings of different approaches *in isolation from one another* through the lens of the criteria of explanatory adequacy for the problem agenda of evolutionary innovation and novelty. Each of the methods has inherent deficiencies and the goal of the next chapter is to begin structuring the project of providing an integrated explanation from the vantage point of a disciplinary synthesis (Evo-devo).

6. INTERPRETATION, COMPARISON, CONSEQUENCES, EVALUATION, AND IMPLICATIONS

6.1. Introduction

The materials for an analysis of conceptual change, defined in terms of conceptual cluster differences, are now in place with respect to the biological concepts of EVOLUTIONARY INNOVATION and NOVELTY. Chapter 1 presented the framework of conceptual clusters and equilibrium states. Conceptual clusters are addressed to problem agendas in the practice of offering explanations of biological phenomena. Chapter 2 provided an account of problem agendas before proceeding to distinguish and characterize the problem agenda of innovation and novelty. In Chapter 3 we fleshed out the abstract idea of a problem agenda by organizing research concerning the origin of avian feathers and flight. A historical investigation was undertaken in Chapter 4 in which we observed distinctive features of explanatory strategies found in comparative embryology, morphology, and paleontology, the primary disciplinary loci for studying innovation and novelty. Chapter 5 described the structure of developmental genetic explanations of innovation and novelty in depth, using two extended case studies. Other approaches were detailed, patterns of disciplinary interrelations were recognized, and resistance to the presupposition of the problem agenda identified.

The goal of this chapter is to bring this material together along four lines: interpretations and comparisons, consequences, evaluation, and implications. ‘Interpretations and

Comparisons' (Section 6.2) concerns the reconstruction of conceptual clusters involved in explanations of evolutionary innovation and novelty and the comparison, both synchronic and diachronic, of these conceptual clusters. The primary observation is that alterations in conceptual clusters are most noticeable with respect to the addition of molecular genetic entities in causal and evidentiary roles. Conceptual change has occurred with respect to *explanations* of innovation and novelty but not with respect to the *concepts* themselves.

'Consequences' (Section 6.3) focuses on the explanatory demands arising from the problem agenda of innovation and novelty as defined in Chapter 2. Dwelling on the criteria of explanatory adequacy for the problem agenda reveals further philosophical issues of interest, such as differences in the kinds of explanations required to explain innovations and novelties. These issues can be isolated from the case studies of Chapter 5. After detailing these consequences, I evaluate ('Evaluation' – Section 6.4) present explanations of innovation and novelty in light of these demands, revisiting the promise of contemporary Evo-devo to make a distinct contribution to explaining the origin of innovations and novelties. To address deficiencies isolated in contemporary explanations of innovation and novelty, I introduce the notion of a 'maximal conceptual cluster'. Instead of simply ascertaining the conceptual clusters of biologists using the problem agenda (a descriptive activity), a model of integrated explanations from disciplinary syntheses is presented that produces a 'maximal' conceptual cluster—the intentional use of multiple concepts that adequately address the criteria of explanatory adequacy. The significance of these results is then discussed in the context of explanatory pluralism and interdisciplinary epistemology.

Finally, Section 6.5 ('Implications') explores the adequacy of current evolutionary theory in light of this analysis. Is it the case that evolutionary theory is somehow inadequate with respect to explaining evolutionary innovations and novelties? How should the structure of evolutionary theory be viewed in light of problem agendas and the synthesis of different biological disciplines to produce integrated explanations? I conclude that evolutionary theory, understood strictly in terms of evolutionary genetics, is in need of revision but that the structure of a multidisciplinary evolutionary theory is unclear. Conceptualizing evolutionary theory in terms of multiple problem agendas is suggested as an organizing principle for an evolutionary theory with multiple disciplinary contributions, which differs from other proposals that include developmental considerations into evolutionary biology (Gould 2002; Walsh 2003).

6.2. Interpretations and Comparisons

6.2.1. Reconstructing Conceptual Clusters

Because the biological details involved in different explanations of innovation and novelty have been documented in earlier chapters, this section concentrates on reconstructing the conceptual clusters in an economical representation with only a question-answer restatement of the particular topic. Conceptual clusters are presented in a modified tabular format that captures four basic features (explanatory target concepts, concepts invoked as causes, concepts invoked evidentially, and other cluster components) and scores for 'type of concept' and 'borrowed versus owned'.[198] The goal is to have multiple conceptual clusters for analysis within the phylogenetic approach to philosophy of science. The patterns within and between these reconstructions are addressed subsequent to their presentation. Minimal commentary accompanies each example.

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[198] Some of the 'concepts' cited are combinations of concepts that do not have a single word or phrase attributed to them. Labeling the overarching category 'concepts/conceptual components' highlights this feature. Conceptual components that are combinations of single word/phrase concepts are implicitly identified by the inclusion of the component concepts within the 'other component' categorization.

If we take our hypothetical neurobiology example from Chapter 1 and assume physiologists are offering the explanation, it would yield the following:

> **Q:** Why does a neuron fire or release its action potential?
>
> **A:** A neuron fires when ion channel protein complexes open successively along an axon and allow a particular kind of ion to enter the cell, propagating a directional electrical impulse, which results in the release of neurotransmitters across a synapse. Evidence for this explanation is garnered by patch clamp techniques that measure the change in electrical potential, molecular genetic analyses that disrupt ion channel function, and biochemical analyses that manipulate ion concentrations. Other considerations include the 'routine' behavior of the ions and the stimulatory effect of an electrical impulse.

Table 3: Conceptual Cluster Reconstruction Example - Neuron Firing

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	NEURON FIRING	Activity	Owned
Cause(s)	ION CHANNEL PROTEIN COMPLEXES OPENING	Activity	Borrowed
	ION MOVEMENT	Activity	Borrowed
	INFLUX OF IONS INTO NEURON	Activity	Borrowed
	ELECTRICAL IMPULSE PROPAGATION	Activity	Owned
Evidence	SUCCESSION / PROPAGATION	Relation (Time / Space)	Owned
	ELECTRIC POTENTIAL CHANGE	Activity	Owned
	ION CHANNEL GENE KNOCKDOWN	Process	Borrowed
	ION CONCENTRATION MANIPULATION	Process	Owned
	NEUROTRANSMITTER RELEASE	Activity	Borrowed
Other Components	NEURON	Entity	Owned
	ION CHANNEL PROTEIN COMPLEXES	Entity	Borrowed
	HAVING ION CHANNEL PROTEIN COMPLEXES	Property	Owned
	ELECTRICAL IMPULSE	Activity	Owned
	ELECTRIC POTENTIAL	Property	Borrowed
	ION	Entity	Borrowed
	PATCH CLAMP	Process	Owned
	ION CHANNEL GENE	Entity	Borrowed
	NEUROTRANSMITTER	Entity	Borrowed

Causal relations are implicitly scored for all concepts counted as ‘causes’ and some spatiotemporal relations are only implicit such as the influx of ions into the neuron. ‘Distance’, the sense of how important a concept is as a cause of the explanatory target concept, is not formally recognized but will be noted in each instance. In the present case, ion protein channel opening is considered the closest because it is the rate-limiting step for the other causes to operate and induce neuronal firing. Recall that the distance measure concerns the importance of a concept in the explanation. This is distinct from relationships among entities picked out by the concepts, such as disparities in levels of organization. Distance concerns which concepts are invoked causally; the relationship among the things these invoked concepts represent and the things represented by explanatory target concepts is another issue.

This hypothetical example has features of interest that may obtain in other explanations. The causes invoked to explain an activity are all activities themselves. All of these activities have entity counterparts, such as the ION in ION FLUX or NEURON in NEURONAL FIRING. The ‘closest’ causal concept invoked is borrowed rather than owned. Physiologists are co-opting the research and methodology of molecular genetics and biochemistry when utilizing ION CHANNEL PROTEINS.

6.2.2. Past Explanations: Conceptual Cluster Reconstruction

6.2.2.1. Medial Brace in Avian Skull (Bock 1959)

> **Q:** How did avian double jaw articulation originate, which prevents the jaw from disarticulating under strong forces during feeding activity (such as skimming for fish)?
>
> **A:** Bony knobs on the basitemporal plate, which serve as attachment points for cervical muscles, were preadapted for the secondary articulation of the medial brace due to their position and projection with respect to the entire basitemporal plate. This secondary basitemporal articulation in the avian mandible (the medial brace) arose during ontogeny

through epigenetic interactions and was subsequently genetically hardwired (genetic assimilation). (Abbreviation: muscle attachment point = MAP)

Table 4: Conceptual Cluster - Avian Double Jaw Articulation

	Concept/Conceptual Component	Type	Borrowed/Owned
Explanatory Target	AVIAN DOUBLE JAW ARTICULATION	Entity	Owned
Cause(s)	CHANGE IN MUSCLES ATTACHED TO MAP	Relation (Space)	Owned
	EPIGENETIC FORMATION OF ATTACHMENT BETWEEN MAP AND CERVICAL MUSCLES	Activity	Borrowed
Evidence	MAP LOCATION (FOR BOTH PRIMARY AND SECONDARY ARTICULATION)	Relation (Space)	Owned
	MAP SIZE (PROJECTION)	Property	Owned
	CERVICAL MUSCLES ATTACHED	Property	Owned
Other Components	AVIAN FEEDING	Activity	Owned
	PREADAPTATION	Property	Owned
	GENETIC ASSIMILATION	Process	Borrowed
	EPIGENETIC FORMATION	Process	Borrowed
	MAPS	Entity	Owned
	BASITEMPORAL PLATE	Entity	Owned
	CERVICAL MUSCLE PERFORMANCE	Activity	Owned
	CERVICAL MUSCLES	Entity	Owned

The epigenetic cause cited for the developmental origin of the attachment between MAPs and cervical muscles does not have a corresponding concept with respect to evidence. The epigenetic formation of this bone-muscle attachment and the process of genetic assimilation are borrowed concepts. The ‘closest’ causal concept is the change in cervical muscles attached to the MAPs, in part because the epigenetic formation of these attachments is not detailed.

6.2.2.2. Origin of Vertebrates from a Modified Ascidian Tadpole (Berrill 1955)

Q: How did the larger sized, proto-vertebrate embryonic form arise from an invertebrate, chordate ancestral form?

A: The invertebrate, chordate ancestral form was most like a larval ascidian because a notochord and dorsal nerve chord can be achieved through neoteny. Ascidians also exhibit canonical deuterostome cleavage, gastrulation, and organogenesis. The increase in size of this proto-vertebrate embryonic form is due to a mechanism of size increase by slippage in the number of cell division cycles relative to gastrulation (either by accelerated cell division or retardation of the onset of gastrulation), which is likely since size variability in ascidians is a consequence of cell size not cell number. Size increase was favorable due to increased dispersal ability and availability of new freshwater habitats.

Table 5: Conceptual Cluster - Proto-Vertebrate Larval Form Size

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	PROTO-VERTEBRATE LARVAL FORM SIZE	Property	Owned
Cause(s)	CHANGE IN GASTRULATION ONSET	Relation (Time)	Owned
	CHANGE IN CELL DIVISION CYCLE TIMING	Relation (Time)	Borrowed
Evidence	ASCIDIAN CELL NUMBER VARIANCE	Property	Owned
	ASCIDAN CELL SIZE INVARIANCE	Property	Owned
	ASCIDIAN ONTOGENY	Process	Owned
	VERTEBRATE ONTOGENY	Process	Borrowed
Other Components	DEUTEROSTOME GASTRULATION	Activity	Owned
	DEUTEROSTOME CLEAVAGE	Activity	Owned
	DEUTEROSTOME ORGANOGENESIS	Activity	Owned
	NEOTENY	Relation (Time)	Owned
	NOTOCHORD	Entity	Owned
	DORSAL NERVE CHORD	Entity	Owned
	PROTO-VERTEBRATE LARVAL FORM	Entity	Owned
	INVERTEBRATE CHORDATE ANCESTRAL FORM	Entity	Owned
	CELL DIVISION	Activity	Borrowed
	CELL	Entity	Borrowed
	DISPERSAL ABILITY	Property	Owned
	‘NEW’ FRESHWATER HABITATS	Entity	Borrowed

The target of Berrill’s explanation was a property (size) rather than an entity (morphology) of the proto-vertebrate. Borrowed concepts concern cellular phenomena but also include the conception of vertebrate ontogeny derived from other researchers. The causes invoked are forms of heterochrony with no particular ‘close’ causal concept. Berrill also includes an ecological background relevant to the property being explained.

6.2.2.3. Major Anatomical Differences of the Giant Panda (Davis 1964)

> **Q:** How did the major anatomical differences of the giant panda, in contrast to other bears, originate (e.g. skull, enlarged radial sesamoid, skeletal morphology, and dentition)?
>
> **A:** These differences are largely a consequence of epigenetic mechanisms such as external mechanical forces impinging during ontogeny, as well as pleiotropic effects of a small number of genetic mutations, which are related to timing changes in relative growth rates, thereby leading to allometry, and differentiation events. Support for this arises from the non-functional aspects of the morphology, proportional allometric relationships (length of tibia vs. length of femur and pelvic breadth vs. pelvic length), the ability to elucidate the skull changes via transformation grids with deformed cartesian coordinates, biomechanics of carnivorous and herbivorous mastication, especially as observed in other bear species inclined to herbivory, morphogenetic mechanisms of mammalian skull units drawn from studies of cranial development in bulldogs and the details known about the vertebrate limb ontogeny, and developmental fields or gradients in dental ontogeny.

Table 6: Conceptual Cluster - Giant Panda Anatomical Features

	Concept/Conceptual Component	Type	Borrowed/Owned
Explanatory Target	GIANT PANDA ANATOMICAL FEATURES	Entity	Owned
Cause(s)	CHANGE IN TIMING OF GROWTH	Relation (Time)	Borrowed
	CHANGE IN TIMING OF DIFFERENTIATION	Relation (Time)	Borrowed
	EPIGENETIC INTERACTIONS DUE TO EXTERNAL MECHANICAL FORCES	Activity	Borrowed
	PLEIOTROPIC INTERACTIONS OF GENE MUTATIONS	Activity	Borrowed
Evidence	ALLOMETRY	Relation (Space)	Owned
	NON-FUNCTIONALITY	Property	Owned
	CRANIAL ONTOGENY (BULLDOG, TETRAPOD LIMB)	Process	Borrowed
	CARTESIAN COORDINATE TRANSFORMATION	Process	Owned
	MASTICATION	Activity	Owned
Other Components	HERBIVORY / CARNIVORY	Activity	Owned
	BULLDOG	Entity	Borrowed
	TETRAPOD LIMB	Entity	Borrowed
	SPECTACLED BEAR	Entity	Owned
	MORPHOGENETIC FIELD	Entity	Borrowed
	SKULL	Entity	Owned
	ENLARGED RADIAL SESAMOID	Entity	Owned
	SKELETAL MORPHOLOGY	Entity	Owned
	DENTITION	Entity	Owned
	PLEIOTROPY	Activity	Borrowed
	GENE / MUTATION	Entity	Borrowed
	DIFFERENTIATION	Activity	Borrowed
	FEMUR / PELVIS / TIBIA	Entity	Owned
	MECHANICAL FORCE	Activity	Owned

Davis's overall explanation of the anatomical differences in the giant panda exclusively uses borrowed concepts as causes for their origination. This also obtains for corresponding concepts in the evidential (CRANIAL ONTOGENY) and other category (MORPHOGENETIC FIELD). Epigenetic interactions due to mechanical forces are causally more 'close' than pleiotropy.

6.2.2.4. Origin of Vertebrates from Invertebrate Taxa (Gregory 1946)

> **Q:** How did the proto-vertebrate form emerge from an invertebrate, ancestral form?
>
> **A:** Attached or slow-moving food sifters (invertebrate ancestral form) were transformed into swift-moving predators (proto-vertebrate form) via neoteny through a precise transition of a carpoid echinoderm form to a balanoglossid hemichordate form to an ascidian urochordate form to an amphioxus cephalochordate form. In this sequence the larvae become more motile and the adults lose their sessile habits. Specifically, the neoteny concerns accelerated sexual maturity of gonads in the locomotory stage of the cephalochordate form, eliminating a metamorphic transition to a less active adult form.

Table 7: Conceptual Cluster - Proto-Vertebrate Form

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	PROTO-VERTEBRATE FORM	Entity	Owned
Cause(s)	NEOTENY	Relation (Time)	Borrowed
Evidence	ADULT FEEDING	Activity	Borrowed
	LARVAL MOTILITY	Activity	Borrowed
	MORPHOLOGICAL SEQUENCE	Relation (Space/Time)	Owned
Other Components	GONADS	Entity	Borrowed
	PROTO-VERTEBRATE FORM	Entity	Owned
	INVERTEBRATE ANCESTRAL FORM	Entity	Owned
	CARPOID ECHINODERM	Entity	Borrowed
	BALANOGLOSSID HEMICHORDATE	Entity	Borrowed
	ASCIDIAN UROCHORDATE	Entity	Borrowed
	AMPHIOXUS CEPHALOCHORDATE	Entity	Borrowed
	AQUATIC LOCOMOTION	Activity	Owned

Gregory's explanation contains a large number of borrowed conceptual resources. As a vertebrate functional morphologist, this is not surprising. Some of the concepts are owned because Gregory created them: the nature of the PROTO-VERTEBRATE FORM and INVERTEBRATE ANCESTRAL FORM, as well as the MORPHOLOGICAL SEQUENCE among marine invertebrate forms.

6.2.2.5. Origin of the Tetrapod Limb (Westoll 1943b)

Q: How were the ancestral paired appendages of fishes transformed into tetrapod limbs, primarily utilized in terrestrial locomotion?

A: A rhipidistian paddle was transformed into a locomotory appendage through modifications arising from imposing a tetrapod limb position on the rhipidistian paddle with respect to the main body axis (the downward flexing of an extended fin between the first and second mesomeres, and the forward torsion of the part distal to the second mesomere, allowing for the utilization of the first preaxial ray in structural support). Digits are secondarily derived. Evidence is found in basal tetrapod limb structure, locomotory demands and a wider capacity of functional rotation in the fin axis, and developmental studies of existing tetrapod limbs.

Table 8: Conceptual Cluster - Tetrapod Limb

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	TETRAPOD LIMB	Entity	Owned
Cause(s)	CHANGE IN FIN FLEXURE	Relation (Space)	Owned
	CHANGE IN FIN TORSION	Relation (Space)	Owned
	CHANGE IN EMBRYONIC FIELD OF INFLUENCE	Relation (Space)	Borrowed
Evidence	AQUATIC / TERRESTRIAL LOCOMOTION	Activity	Owned
	TETRAPOD LIMB DEVELOPMENT	Process	Borrowed
	BASAL TETRAPOD LIMB FEATURES	Property	Owned
Other Components	MESOMERES	Entity	Borrowed
	TETRAPOD	Entity	Owned
	RHIPIDISTIAN	Entity	Owned
	RHIPIDISTIAN PADDLE	Entity	Owned
	EMBRYONIC FIELD	Entity	Borrowed
	FIN FLEXURE	Activity	Owned
	FIN TORSION	Activity	Owned
	BODY AXIS	Property	Owned
	PREAXIAL RAY	Entity	Owned

The grain of concept use reconstructed could be altered, including Crossopterygii (which includes rhipidistians) or rhipidistian taxa (e.g. *Eusthenopteron*), as well as basal tetrapods (e.g. *Eryops*). This reconstruction seems most appropriate based on Westoll's text. I have also not (i) highlighted the secondary derivation of digits (which he considered new formations arising from developmental rudiments), (ii) distinguished all of the skeletal elements (humerus, ulna) or their groupings (archepodium, neopodium) in the explanation, or (iii) identified the non-rhipidistian fishes used as comparisons for fin locomotory motions. A key pattern emerging is the consistent borrowing of developmental concepts, for the causal and evidential categories.

6.2.3. Historical Comparisons: Similarities and Differences in Conceptual Clusters

A number of interesting similarities emerge in these past explanations. The explanatory target concept is an entity in all but one, which is a property of an entity. The causal concept types are either activities or relations, with the former being some kind of epigenetic dynamics whereas the latter is usually a form of heterochrony. All of the conceptual clusters borrow causal concepts, and borrow them distinctively from developmental considerations. The outlier is Berrill's explanation, which takes from cell biology, not needing to borrow the conceptual resources from development given his own embryological research. All of the explanations except for Gregory's have properties or processes as evidential concepts. There is a large degree of congruity in the structuring of these conceptual clusters: explanatory target concept = entity; causal concepts = activities, relations; evidential concepts = properties, processes; and, 'borrowing' is primarily done from ontogenetic research. This congruence corroborates the close relations already identified in our historical analysis (Chapter 4).

6.2.4. Contemporary Explanations: Conceptual Cluster Reconstruction

6.2.4.1. Avian Feathers: Developmental Genetics (Section 3.2)

Q: How did feathers originate from a reptilian scale-like integument?

A: Feather originated from a reptilian scale-like integument as a consequence of altered spatial and temporal developmental regulatory gene expression patterns of existing genes in the epithelium and mesenchyme of particular body regions, likely due to *cis*-regulatory element sequence evolution. Some relevant gene expression includes: BMPs and Protein Kinase C inhibiting placode formation thereby contributing to feather bud spacing; Shh, Fgfs, Protein Kinase A, TGF β2 are feather bud activators; high β-catenin levels initiate epidermal placode formation, follicle formation, and primary formation of the feather bud (low activity is detected in avian scales); *Wnt-7a* is involved in anterior-posterior asymmetry of the feather, as well as its proximal-distal elongation; interactions among three domains in the feather bud generate feather axis specification and morphology (an anterior domain expressing *Msx-1*, *Msx-2*, and *Hox* genes, a posterior domain expressing *Wnt-7a* and *Delta-1*, and a middle domain expressing *Notch-1* and *Shh*); interactions between Shh and *Bmp2/4* pattern the barb ridges, as well as the barbs and rachis through apoptotic mechanisms; antagonism between BMP4 and Noggin contribute to feather branching. Almost all of this evidence is drawn from developmental studies of chickens.

Table 9: Conceptual Cluster - Avian Feathers

	Concept/Conceptual Component	Type	Borrowed/Owned
Explanatory Target	AVIAN FEATHERS	Entity	Owned/Borrowed
Cause(s)	β-CATENIN INCREASE IN EPIDERMAL PLACODE / FEATHER BUD	Activity	Owned
	NOTCH INCREASE IN EPIDERMAL PLACODE / FEATHER BUD	Activity	Owned
	BMP DECREASE IN EPIDERMAL PLACODE / FEATHER BUD	Activity	Owned
	TRIPARTITE ANTERIOR/POSTERIOR DOMAIN WITH GRADIENTS OF GENE EXPRESSION	Entity	Owned
	APOPTOSIS IN FEATHER BUD (SHH DEPENDENT)	Process	Owned
Evidence	β-CATENIN EXPRESSION / MISEXPRESSION	Property	Owned
	BMP EXPRESSION / MISEXPRESSION	Property	Owned
	PROTEIN KINASE EXPRESSION / MISEXPRESSION	Property	Owned
	SHH EXPRESSION / MISEXPRESSION	Property	Owned
	FGF EXPRESSION / MISEXPRESSION	Property	Owned
	TGF β2 EXPRESSION / MISEXPRESSION	Property	Owned
	NOTCH/DELTA EXPRESSION / MISEXPRESSION	Property	Owned
	HOX EXPRESSION / MISEXPRESSION	Property	Owned
	WNT EXPRESSION / MISEXPRESSION	Property	Owned
	MSX EXPRESSION / MISEXPRESSION	Property	Owned
Other Components	REPTILIAN INTEGUMENT	Entity	Borrowed
	CHICK	Entity	Borrowed
	HETEROTOPY / HETEROCHRONY	Relation (Time / Space)	Owned
	CIS-REGULATORY ELEMENT	Entity	Owned
	EPIDERMAL PLACODE	Entity	Owned
	FEATHER BUD	Entity	Owned
	FEATHER FOLLICLE	Entity	Owned
	PLACODE FORMATION	Activity	Owned
	BARBS	Entity	Owned
	RACHIS	Entity	Owned
	ANTERIOR/POSTERIOR – PROXIMAL/DISTAL	Relation (Space)	Owned
	AXIS SPECIFICATION	Process	Owned
	β-CATENIN, BMP. DELTA, FGF, HOX, MSX, NOTCH, PROTEI KINASE, SHH, TGF β2, WNT	Entity	Owned

The status of the explanatory target concept as ‘owned or borrowed’ arises from the difference between treating feather tracts or individual feathers as the *explanandum* phenomena. The ‘owned’ understanding is individual feathers whereas the ‘borrowed’ is feather tracts, the latter of which is derived from comparative anatomy. There is a lot of documented gene expression in the conceptual cluster, which means a lot of molecular entities are invoked.

6.2.4.2. Avian Flight: Functional Morphology / Paleontology (Section 3.3)

> **Q:** How did avian flight originate?
>
> **A:** Avian flight originated in bipedal theropod-like dinosaurs. The production of a flight stroke to generate the lift or thrust needed for powered flight was accomplished via a functional switch from a predatory stroke to a flight stroke via multiple skeletal, neurological, and behavior alterations: elongated hands were protracted along the joint of the semilunate carpal (allowing protraction, retraction, and rotation); further elongation of arms and hands changed shoulder joint orientation; innervations altered for flight stroke function along with behavioral modifications; and, elaboration of feathers produced a competent airfoil. Evidence is derived from the identification of relevant modifications of these features (dromaeosaurids have the sideways-flexing wrist joint that is a prerequisite for the flapping of wings to produce thrust and appropriate shoulder girdle modifications, hollowing of long bones, removal of a weight supporting role for pedal digit I, overall body size reduction, and expansion of the coracoid and sternum for increased attachment and number of pectoral muscles required for a flight stroke), biomechanical analyses of flight in extant and extinct taxa (demonstration that non-avian maniraptoriforms such as *Archaeopteryx* could generate thrust from flapping motion and that thrust is more critical than lift to achieving flapping flight from the ground-up), and observations on wing-assisted incline running in juvenile and adult birds.

Table 10: Conceptual Cluster - Avian Flight

	Concept/Conceptual Component	Type	Borrowed/Owned
Explanatory Target	AVIAN FLIGHT	Activity	Owned
Cause(s)	PROTRACTION ALONG SEMINLUNATE CARPAL JOINT	Relation (Space / Time)	Owned
	ARM AND HAND ELONGATION	Relation (Space / Time)	Owned
	BEHAVIOR CHANGES	Relation (Space / Time)	Owned
	ALTERED INNERVATIONS	Relation (Space / Time)	Owned
	FEATHER ELABORATION	Relation (Space / Time)	Owned
Evidence	DROMAEOSAURID SIDEWAYS-FLEXING WRIST JOINT	Entity	Owned
	DROMAEOSAURID SHOULDER GIRDLE	Entity	Owned
	ARCHAEOPTERYX FLIGHT STROKE	Process	Owned
	LONG BONE HOLLOWING	Property	Owned
	DECREASED BODY SIZE	Property	Owned
	PEDAL DIGIT 1 FUNCTION	Activity	Owned
	CORACOID SIZE INCREASE	Property	Owned
	STERNUM SIZE INCREASE	Property	Owned
	WING-ASSISTED INCLINE RUNNING	Activity	Owned
Other Components	THEROPOD	Entity	Owned
	LIFT / THRUST	Entity	Owned
	DROMAEOSAURID	Entity	Owned
	ARCHAEOPTERYX	Entity	Owned
	SEMINLUNATE CARPAL JOINT	Entity	Owned
	PEDAL DIGIT 1	Entity	Owned
	BONE	Entity	Owned
	CORACOID / STERNUM	Entity	Owned
	FLIGHT STROKE / BEHAVIOR	Activity	Owned
	SHOULDER GIRDLE	Entity	Owned
	FEATHER	Entity	Owned
	INNERVATIONS	Entity	Owned

This cluster has all ‘owned’ concepts but it is an amalgam of two related disciplinary approaches.[199] All of the causes cited are relations between properties of ancestral and descendant taxa; i.e., they are correlations. They might be labeled processes but they are not well characterized. The structure of the explanation is clear as numerous entities are shown to have particular properties that underwrite the *correlations* cited for the origin of flight.

6.2.4.3. Crustacean Mouthparts: Developmental Genetics (Abzhanov and Kaufman 2000b; Averof and Patel 1997)

Q: How did crustacean mouthpart maxillipeds originate?

A: Mouthpart maxillipeds arose from thoracic legs as a consequence of altered spatial and temporal developmental regulatory gene expression patterns of existing genes. Some of the relevant gene expression patterns include: *Ubx* and *AbdA* are repressed in crustacean maxillipeds whereas other crustaceans without maxillipeds have *Ubx* and *AbdA* expressed in thoracic legs (an overall posterior shift in expression early in development); and, high levels of Scr protein accumulate in the anterior appendages of *Porcellio scaber* via posttranscriptional modification in conjunction with their transformation into maxillipeds.

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[199] It might be disputed that these taxa are partly the domain of systematics. While technically accurate, systematics without a paleontological contribution would not have concepts of extinct taxa.

Table 11: Conceptual Cluster - Crustacean Mouthparts

	Concept/Conceptual Component	Type	Borrowed/Owned
Explanatory Target	CRUSTACEAN MOUTHPART MAXILLIPEDS	Entity	Borrowed
Cause(s)	RESTRICTION OF *UBX* EXPRESSION	Activity	Owned
	RESTRICTION OF *ABDA* EXPRESSION	Activity	Owned
	ACCUMULATION OF SCR PROTEIN	Activity	Owned
Evidence	ABSENCE OF *UBX* AND *ABDA* IN MAXILLIPEDS	Property	Owned
	PRESENCE OF *UBX* AND *ABDA* IN THORACIC LEGS	Property	Owned
	MRNA VS. PROTEIN DISCREPANCY FOR SCR IN PROTO-MAXILLIPED APPENDAGE	Property	Owned
Other Components	*UBX*	Entity	Owned
	ABDA	Entity	Owned
	SCR (*MRNA AND PROTEIN*)	Entity	Owned
	THORACIC LEGS	Entity	Borrowed
	MAXILLIPEDS	Entity	Borrowed
	INSECT	Entity	Borrowed
	CRUSTACEAN	Entity	Borrowed
	PORCELLIO SCABER	Entity	Borrowed
	POST-TRANSCRIPTIONAL REGULATION	Process	Owned
	HETEROTOPY / HETEROCHRONY	Relation (Space / Time)	Owned

The multiple crustacean taxa used by Averof and Patel to establish the *Ubx* and *AbdA* expression patterns have been excluded. Note that the developmental regulatory change (for *Scr*) is not a *cis*-regulatory transcriptional control mechanism. The authors saw this as a unique feature of their study thereby reinforcing the emphasis on *cis*-regulatory sequence modification in developmental genetic explanations of innovation and novelty. This conceptual cluster shares a feature with that for avian feather origination: causes and evidence are all ‘owned’ concepts while the explanatory target concept is borrowed. This also holds for the next example.

6.2.4.4. Origin of Vertebrate Jaws: Developmental Genetics (Section 5.3)

Q: How did vertebrate jaws arise from an agnathan ancestral condition?

A: A vertebrate jaw structure arose as a consequence of the altered spatial and temporal developmental regulatory gene expression patterns of existing genes or duplicates in the anterior most branchial arches and other rostral cranial regions, likely due to *cis*-regulatory element sequence evolution. Some relevant gene expression patterns include: the restriction/absence of *Hox* expression from the anterior neural crest cells and branchial arches of gnathostomes; the duplication and divergence of *Dlx* genes into a nested proximal-distal pattern that differentiates the branchial arches (other components, such as *bapx1* and *dHAND*, involved in axial differentiation within individual arches fits into this scheme); *Fgf8* and *Bmp4* antagonistic signaling upstream of *Dlx*, *Msx*, and others has been heterotopically shifted from a more expanded domain inclusive of the post-optic region in lampreys to a maxillomandibular domain only in gnathostomes. This evidence is garnered from the developmental studies of chickens, mice, and zebrafish (gnathostomes) and lampreys (agnathans) including functional studies of misexpression for the genes listed.

Table 12: Conceptual Cluster - Vertebrate Jaws

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	VERTEBRATE JAWS	Entity	Borrowed
Cause(s)	RESTRICTION OF *HOX* EXPRESSION	Activity	Owned
	DLX DUPLICATION	Process	Owned
	DLX NESTED PROXIMODISTAL EXPRESSION	Activity	Owned
	MAXILLOMANDIBULAR *FGF8* AND *BMP4* EXPRESSION	Activity	Owned
	BAPX1 AND *DHAND* ARCH EXPRESSION	Activity	Owned
Evidence	*HOX* MISEXPRESSION IN BRANCHIAL ARCHES	Property	Owned
	HOX EXPRESSION PATTERN IN BRANCHIAL ARCHES AND NEURAL CREST CELLS	Property	Owned
	DLX MISEXPRESSION IN BRANCHIAL ARCHES	Property	Owned
	DLX PARALOGY	Relation (Space)	Owned
	LAMPREY *FGF8* AND *BMP4* POST-OPTIC EXPRESSION	Property	Owned
Other Components	GNATHOSTOME / AGNATHAN	Entity	Borrowed
	BRANCHIAL ARCHES	Entity	Owned
	NEURAL CREST CELLS	Entity	Owned
	MAXILLOMANDIBULAR DOMAIN	Entity	Owned
	POST-OPTIC REGION	Entity	Owned
	CHICK	Entity	Borrowed
	MICE	Entity	Borrowed
	ZEBRAFISH	Entity	Borrowed
	LAMPREY	Entity	Borrowed
	CIS-REGULATORY ELEMENT	Entity	Owned
	HETEROTOPY / HETEROCHRONY	Relation (Space / Time)	Owned

The taxon and grouping concepts utilized in this developmental genetic explanation are borrowed, as well as the explanatory target concept (as in the previous example). Another pattern emerging for developmental genetic explanations is that the predominant causal concepts are activities (gene expression), which are used to explain an entity (evolutionary novelty).

6.2.4.5. Forelimb Structure in Salamanders: Comparative Development (Alberch and Alberch 1981; Hanken 1985; Hanken and Wake 1993)

Q: How did the limb morphology of some plethodontid salamander taxa arise (fully webbed hands/feet, reduction/loss of phalangeal elements, fusion of carpals and tarsals)?

A: An overall truncation of development (leading to miniaturization) in some plethodontid taxa (e.g. *Bolitoglossa* and *Thorius*) occurred due to global heterochrony via paedomorphosis, most likely early maturation (progenesis), which can be traced back to a truncation in the developmental trajectories for these different limb features (e.g. inter-digital apoptosis occurs late in development. Truncating limb development would lead to increased webbing of hands and feet). Other evidence is derived from truncated development in other skeletal features, such as the skull, as well as a lack of ossification and a lack of functional correlation for affected morphological features (e.g. decreased number of separate cartilages without change in ecology or locomotory shift).

Table 13: Conceptual Cluster – Salamander Limb Features

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	LIMB FEATURES	Entity	Owned
Cause(s)	HETEROCHRONY	Relation (Time)	Owned
	PROGENESIS (EARLY MATURATION)	Process	Owned
	GROWTH TERMINATION	Activity	Owned
	DEVELOPMENTAL TRAJECTORY TRUNCATION	Activity	Owned
Evidence	WEBBED HANDS/FEET	Entity	Owned
	INTERDIGITAL APOPTOSIS	Process	Borrowed
	FEWER CARTILAGES	Property	Owned
	CARPAL / TARSAL FUSION	Process	Borrowed
	REDUCTION / LOSS OF PHALANGEAL ELEMENTS	Process	Owned
	LACK OF OSSIFICATION	Property	Owned
	CRANIAL MORPHOLOGY DIFFERENCES	Property	Owned
	NO ECOLOGICAL / FUNCTIONAL SHIFT	Property	Owned
Other Components	PLETHODONTID SALAMANDERS	Entity	Borrowed
	BOLITOGLOSSA	Entity	Borrowed
	THORIUS	Entity	Borrowed
	MATURATION	Process	Owned
	DEVELOPMENTAL TRAJECTORY	Entity	Owned
	OSSIFICATION	Process	Borrowed
	CARPAL / TARSAL	Entity	Owned
	PHALANGEAL ELEMENTS	Entity	Owned
	LOCOMOTION	Activity	Owned

The causal and evidential concepts are a mixture of owned and borrowed but some developmental concepts are owned. PROGENESIS is the 'closest' causal concept because it is necessary to induce the termination of growth and truncation of developmental trajectories.

6.2.4.6. Body Plan Origination: Epigenetics (Newman and Müller 2000)

> **Q:** How did body plans that characterize phyla originate?
>
> **A:** Body plans arose as a result of external physicochemical factors impinging on the soft, excitable matter of cells and tissues similar to the effects observed in polymorphisms and phenotypic plasticity in present species. These factors are epigenetic (conditional, nonprogrammed determinants of ontogeny) and include interactions with cell metabolism, tissue masses based on physical laws of condensed materials, and tissue masses among themselves. Differential cell adhesion produces preferential patterns during random cell movement such as cell polarity, lumen formation, multilayering, segments, and branched structures. The construction of these body plans using multiple patterns, pathways, and networks of gene expression is a secondary phenomenon, akin to genetic assimilation.

Table 14: Conceptual Cluster - Body Plans

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	BODY PLAN	Entity	Borrowed
Cause(s)	PHYSICOCHEMICAL FACTOR EFFECTS ON SOFT, EXCITABLE MATTER	Activity	Owned
Evidence	DIFFERENTIAL CELL ADHESION	Property	Owned
	MODULATION OF CELL ADHESION BY ION CONCENTRATION	Process	Borrowed
	MORPHOLOGICAL OUTCOMES OF DIFFERENTIAL CELL ADHESION	Property	Owned
	MODULATION OF CELL METABOLISM BY ION CONCENTRATION	Process	Borrowed
	TISSUE INTERACTIONS DURING ONTOGENY	Process	Owned
	PHENOTYPIC PLASTICITY	Property	Borrowed
	POLYMORPHISM	Property	Borrowed
	GENETIC ASSIMILATION	Process	Borrowed
Other Components	SOFT, EXCITABLE MATTER	Entity	Borrowed
	CELLS	Entity	Owned
	TISSUES	Entity	Owned
	EPIGENETIC / GENETIC	Property	Owned
	PHYSICOCHEMICAL FACTOR / ION	Entity	Borrowed
	EXTERNAL / INTERNAL	Relation (Space)	Owned
	CELL POLARITY	Property	Owned
	LUMEN FORMATION	Activity	Owned
	MULTILAYERING	Property	Owned
	SEGMENTS	Property	Owned
	BRANCHED STRUCTURES	Entity	Owned

This explanation is executed at a highly abstract level, as it does not aim to explain a particular novelty but rather many simultaneously. The evidence is drawn from a variety of existing species. It is applied to an evolutionary/historical juncture (not a phylogenetic juncture) that is proposed to be discontinuous with the present in terms of the mechanisms responsible for the developmental production of form. Evidence concerns either general properties of entities or widespread processes, which is required to be applicable to the origin of different body plans.

6.2.4.7. Teleost Endothermy: Functional Morphology (Block 1991)

Q: How did endothermy originate within several species of Scombroidei fishes (e.g. tuna or swordfish)?

A: Endothermy arose as a result of highly oxidative skeletal muscle modification coupled with preexisting large body size. In tunas, endothermy was the result of an internalization of oxidative muscle mass along with the insertion of a counter-current heat exchanger into the circulation of this muscle mass to reduce conductive and convective heat loss. In billfishes (e.g. swordfish), brain temperature is elevated due to the presence of a heat-generating organ underneath the brain along with a counter-current heat exchanger derived from carotid circulation. The heat-generating organ is a modification of the superior rectus muscle with novel muscle fiber types (lacking myofibrillar lattice) and increased amounts of Ca^{2+} ATPase for calcium cycling. Supporting evidence includes the high mitochondrial volume of teleost oxidative muscle and the high concentration of myoglobin in Scombroidei red muscle.

Table 15: Conceptual Cluster - Teleost Endothermy

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	TELEOST ENDOTHERMY	Activity	Owned
Cause(s)	MUSCLE MASS INTERNALIZATION	Relation (Space)	Owned
	COUNTER CURRENT HEAT EXCHANGER	Entity	Owned
	SUPERIOR RECTUS MODIFICATION	Property	Owned
	BODY SIZE	Property	Owned
Evidence	MITOCHONDRIAL VOLUME OF OXIDATIVE MUSCLE	Property	Borrowed
	HEAT GENERATING ORGAN	Entity	Owned
	MYOGLOBIN MUSCLE CONCENTRATION	Property	Borrowed
	MUSCLE FIBER LACKING MYOFIBRILLAR LATTICE	Property	Owned
	INCREASED CA^{2+} ATPASE	Property	Owned
Other Components	SUPERIOR RECTUS	Entity	Owned
	OXIDATIVE MUSCLE	Entity	Owned
	MUSCLE FIBER	Entity	Owned
	TELEOST	Entity	Borrowed
	SCAMBROIDEI	Entity	Borrowed
	TUNA	Entity	Borrowed
	BILLFISHES	Entity	Borrowed
	MYOGLOBIN	Entity	Borrowed
	MITOCHONDRIA	Entity	Borrowed
	MYOFIBRILLAR LATTICE	Property	Owned
	CALCIUM CYCLING	Process	Borrowed
	CA^{2+} ATPASE	Entity	Borrowed
	OXIDATIVE METABOLISM	Process	Borrowed
	CAROTID CIRCULATION	Process	Owned

Besides the taxa utilized, the key borrowed concepts are biochemical and physiological. Another feature is the citation of properties of particular entities. The SUPERIOR RECTUS MODIFICATION and MUSCLE MASS INTERNALIZATION are ‘closer’ than both BODY SIZE and the presence of a COUNTER-CURRENT HEAT EXCHANGER, the latter of which is considered closer than the former.

6.2.4.8. Origination of Dorsal Ridge Scale Patterns: Paleontology (McCune 1990)

Q: How did the different patterns of dorsal ridge scaling in semionotid fishes arise?

A: The developmental program routinely produced anomalous variation in ridge scale patterns during the early formation and expansion of the lake habitat. Evidence for this comes from the existence of dorsal ridge scale anomalies within individuals that are characteristic of entire species, some of which are atavisms or supernumerary scales, in the early phase of lake formation and colonization. (Dorsal ridge scale anomalies are more abundant in older lake sediments.) Thus, there are parallels between ancestral intraspecific variation and derived interspecific variation.

Table 16: Conceptual Cluster - Dorsal Ridge Scale Patterns

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	DORSAL RIDGE SCALE PATTERNS	Property	Owned
Cause(s)	DEVELOPMENTAL PROGRAM	Activity	Borrowed
Evidence	DORSAL RIDGE SCALE PATTERN ANOMALIES	Property	Owned
	INTERSPECIFIC VARIATION (YOUNGER)	Property	Owned
	INTRASPECIFIC VARIATION (OLDER)	Property	Owned
	ATAVISM	Process	Borrowed
Other Components	SEMIONOTID	Entity	Owned
	DORSAL RIDGE SCALES	Entity	Owned
	INTRASPECIFIC / INTERSPECIFIC	Relation (Space)	Owned
	SEDIMENT	Entity	Owned
	LAKE FORMATION	Process	Borrowed
	LAKE COLONIZATION	Process	Borrowed
	OLDER / YOUNGER	Relation (Space / Time)	Owned

The primary causal concept in this cluster is borrowed. DEVELOPMENTAL PROGRAM is categorized as an activity rather than process because it is not well characterized. This example exhibits the conceptual blurring between evolutionary novelty and key innovation. The author cites relaxed selection as responsible for the production of the anomalies via a developmental program disruption but relaxed selection cannot ‘disrupt’ a developmental program. It might allow more kinds of variation to persist but it could not be causally responsible for the novel dorsal scale ridge pattern variation observed intraspecifically in older sediments.

6.2.4.9. Origin of Avian Foraging Strategies: Behavioral Biology (Lefebvre and Bolhuis 2003)

Q: How do novel avian foraging strategies originate?

A: Avian feeding innovations originate via existing behavioral flexibility. This is tightly correlated with forebrain size, specifically the hyperstriatum ventrale in the dorsal ventricular ridge. Species able to innovate foraging strategies are at an advantage in the ability to invade new environments, which is connected with the ability to feed near novel objects. The connection between behavioral innovation and forebrain size also holds in primates. These new behaviors can be faithfully transmitted to future generations.

Table 17: Conceptual Cluster - Avian Foraging Strategies

	Concept/Conceptual Component	Type	Borrowed/Owned
Explanatory Target	AVIAN FORAGING STRATEGIES	Activity	Owned
Cause(s)	BEHAVIORAL FLEXIBILITY	Activity	Owned
	LEARNING ABILITY	Property	Owned
Evidence	FOREBRAIN SIZE	Process	Owned
	ABILITY TO FEED NEAR NOVEL OBJECTS	Property	Owned
	ABILITY TO INVADE NEW ENVIRONMENTS	Property	Owned
Other Components	HYPERSTRIATUM VENTRALE	Entity	Owned
	DORSAL VENTRICULAR RIDGE	Entity	Owned
	FORAGING	Activity	Owned
	BIRD	Entity	Borrowed
	PRIMATE	Entity	Borrowed
	ENVIRONMENT	Entity	Owned
	FEEDING	Activity	Borrowed
	LEARNING	Activity	Borrowed

Several of the causal and evidential concepts refer to capacities and learning can be considered psychobiological development. The key causal concept is BEHAVIORAL FLEXIBILITY, which makes contact with phenotypic plasticity studies of functional variation.

6.2.4.10. Origin of Direct Development in Echinoids: Ecology and Environment (Heyland and Hodin 2004; Heyland, Reitzel and Hodin 2004)

Q: How did direct development in specific echinoid lineages originate?

A: Indirect developing echinoid larvae (*Dendraster excentricus, Leodia sexiesperforata*) accumulate thyroid hormone through feeding on planktonic algae (exogenous source) whereas direct developing echinoid nonfeeding larvae (*Peronella japonica*) are able to produce their own thyroid hormone (endogenous source). Thyroid hormone accelerates the transition to metamorphosis in echinoid larvae and its manipulation in indirect developers either retards metamorphosis (decreased thyroxine) or accelerates metamorphosis (increased thyroxine). Accelerated metamorphosis is also observed for indirect developing larvae reared under high food conditions (i.e. high exogenous source of thyroid hormone). Direct development originated as a result of an increased ability (upregulation) to endogenously produce thyroid hormone (a preadaptation for direct development not found in all echinoid lineages), most likely in conjunction with increased egg size and a food starved habitat.

Table 18: Conceptual Cluster - Echinoid Direct Development

	Concept/Conceptual Component	**Type**	**Borrowed/Owned**
Explanatory Target	ECHINOID DIRECT DEVELOPMENT	Process	Owned
Cause(s)	ENDOGENOUS THYROID HORMONE PRODUCTION	Activity	Borrowed
	UPREGULATION	Activity	Owned
	INCREASED EGG SIZE	Property	Owned
	FOOD POOR ENVIRONMENT	Property	Owned
Evidence	THYROID HORMONE MANIPULATION	Process	Owned
	EXOGENOUS FOOD MANIPULATION	Process	Owned
	CHANGE IN METAMORPHOSIS ONSET	Relation (Time)	Owned
Other Components	INDIRECT / DIRECT DEVELOPMENT	Process	Owned
	METAMORPHOSIS	Process	Owned
	THYROID HORMONE / THYROXINE	Entity	Borrowed
	ENDOGENOUS / EXOGENOUS	Relation (Space)	Borrowed
	ECHINOID	Entity	Borrowed
	DENDRASTER EXCENTRICUS	Entity	Borrowed
	LEODIA SEXIESPERFORATA	Entity	Borrowed
	PERONELLA JAPONICA	Entity	Borrowed
	PREADAPTATION	Property	Owned
	LARVAL FEEDING	Entity	Owned
	PLANKTONIC ALGAE	Entity	Borrowed
	EGG	Entity	Owned

As in earlier examples, we can see an ordering of 'closeness' among the causal concepts with UPREGULATION and FOOD POOR ENVIRONMENT being closer than INCREASED EGG SIZE or ENDOGENOUS THYROID HORMONE PRODUCTION. There is overlap with comparative development in this example, as well as physiology.

6.2.4.11. Origin of New Genes: Molecular Biology and Genetics (Wang *et al.* 2000)

Q: How did the *Drosophila* gene *Jingwei* originate?

A: *Jingwei* originated through chimeric fusion of two existing genes, *alcohol dehydrogenase* (*adh*) and a duplicate copy of the gene *yellow emperor* (*ymp*) named *yande*, via exon shuffling in the common ancestor of two African Drosophila species (*yakuba* and *teissieri*). Evidence is derived from the exon structure of *jingwei*, which shares strong sequence similarity with parts of both *adh* and *ymp*, as well as comparison with *ymp* 'normal' paralogue sequence and regulation. *Jingwei* mimics *ymp* testis-specific expression (expected given the chimeric gene structure: 5'*yande*—*adh*3').

Table 19: Conceptual Cluster - *Jingwei* Gene

	Concept/Conceptual Component	Type	Borrowed/Owned
Explanatory Target	*JINGWEI*	Entity	Owned
Cause(s)	EXON SHUFFLING	Activity	Owned
	GENE DUPLICATION	Process	Owned
	RETROTRANSPOSITION	Activity	Owned
Evidence	*JINGWEI* EXON SEQUENCE	Property	Owned
	ADH EXON SEQUENCE	Property	Owned
	YMP EXON SEQUENCE	Property	Owned
	SEQUENCE SIMILARITY	Relation (Space)	Owned
	TESTIS-SPECIFIC *JINGWEI* EXPRESSION	Property	Owned
Other Components	*ADH*	Entity	Owned
	YMP	Entity	Owned
	YANDE	Entity	Owned
	DROSOPHILA YAKUBA	Entity	Borrowed
	DROSOPHILA TEISSERI	Entity	Borrowed
	PARALOGY	Relation (Space)	Owned
	TESTIS-SPECIFIC *YMP* EXPRESSION	Activity	Owned
	EXON / INTRON	Entity	Owned

One aspect of this cluster is the relative lack of borrowed concepts. Besides the species from which the genes are isolated, all of the concepts are derived from the disciplinary nexus where the explanation is found. In contrast to the other conceptual clusters, a very different set of causal concepts having little to do with developmental processes is deployed.

6.2.5. Comparisons: Conceptual Cluster Similarity and Difference, Past and Present

Two global observations are in order before turning to further comparisons. First, a wide diversity of particular concepts and concept kinds play roles in these explanations. This is expected given the number of different disciplinary approaches canvassed. But it is a reminder that if these different phenomena are all evolutionary innovations and novelties, then an adequate explanatory framework for addressing them will require a similar breadth of conceptual resources. We can extend this observation to the *use* of concepts (Section 1.2.1) and recognize different uses by various disciplinary approaches (Stotz and Griffiths 2004). An adequate explanatory framework requires diverse conceptual resources and a strategy to navigate differences in their utilization.

The second observation concerns the disciplinary approach of systematics. Taxon concepts in conceptual clusters were scored as borrowed (from systematics), except in the case of paleontology. We did not specifically discuss the structure of systematics as a disciplinary approach. This was a consequence of our dual-aspect explication (pattern and process) of explanations of innovation and novelty.

6.2.5.1. Synchronic and Diachronic Comparisons of Conceptual Clusters

Some of the similarities among the past conceptual clusters are also shared by present explanations. The explanatory target concept is usually an entity (six entities, three activities, one property, and one process) and the causal concept is typically an activity or a relation. The citation of activities is much greater than relations and if multiple causes are cited activities are usually 'closer'. Properties and processes are again predominant in the evidential concepts. In most conceptual clusters the number of 'other components' is relatively large in contrast to the causal and evidential categorizations. There is a preponderance of entities over other concept types in this category. The number of component types increases in developmental genetic or molecular biological disciplinary approaches as a result of more molecular entities referred to, such as particular genes or cellular components.

One set of differences emerges from the issue of whether particular categories are owned or borrowed. Developmental genetics and epigenetics are alone in having their explanatory target concepts borrowed. Observing this is important because an explanatory target concept usually arises within a field of investigation. Investigative kind concepts (cf. Brigandt 2003; Griffiths 2004) are proposed to serve as groupings of phenomena from one's primary research domain. This feature corroborates the historiographic discussion in Chapter 4 regarding the difference between problems and tools. Old morphological problems from disciplines where the explanatory target concept originated are being investigated with molecular causes and evidence using a new set of tools from a different disciplinary nexus. Molecular biology/genetics and behavior do not borrow any concepts in their clusters, which might indicate that these studies are relatively self-contained within their disciplinary approaches. This makes sense for the former, where the phenomena are all molecular and cellular. Behavior draws on psychobiological development when invoking learning ability but notably it is a capacity (property) rather than a process; what underwrites the capacity or its full range of expression is not documented.

Turning to diachronic comparisons, one similarity of interest for comparative embryology/development, morphology, and paleontology is the stability of their conceptual cluster structure over the time period considered. This qualifies as an equilibrium state in the conceptual clusters of these coordinate disciplinary approaches. Besides the consistent borrowing of causal concepts from developmental considerations, another stable feature is the appeal to relations or properties (as causal preconditions) in their causal concept category. I interpret this in terms of a conflation between the pattern and process aspects of explanations of innovation and novelty. In some cases it may be more appropriate to judge these explanations regarding the establishment of non-homology and phylogenetic juncture rather than the mechanistic origin of variation. This fits with the consistent borrowing of ontogenetic concepts to underwrite the causal component of the clusters. Understanding this particular pattern emphasizes the need to make these two aspects of the explanation explicit. One theoretical development that has facilitated the ability to do this is the widespread adoption of phylogenetic systematics (Hull 1988b; cf. Mishler 2003; Telford and Budd 2003). The disciplinary practice of systematics has been formally separated from its disciplinary 'kin' of comparative embryology, morphology, and paleontology.

One critical difference between conceptual clusters past and present is the reliance on sub-cellular entities and activities in different categories. The molecularization of biology in the past four decades (cf. Morange 1998), but most especially the molecular genetic turn in developmental biology that occurred in the late 1970s/early 1980s (Fraser and Harland 2000), has fundamentally altered the conceptual cluster components. The citation of genes playing a causal role in developmental processes to generate variation relevant to innovation and novelty is observable earlier, such as the 'rate genes' of Huxley and Goldschmidt (Goldschmidt 1945; Huxley 1993 [1932]), but it is not predominant. It is actually peripheral to earlier studies of evolutionary innovation and novelty. The discrepancy is visible in the borrowing of the explanatory target concepts while using owned causal and evidential concepts from developmental genetics. Other contemporary studies bear this out, such as investigations of the tetrapod limb, where paleontological and morphological workers have actively tried to incorporate and assimilate these conceptual resources.

But it is not only a reliance on these concepts that is significant. Their proliferation is a factor as well. Although the number of concepts used by other disciplinary approaches has increased somewhat, there has been an explosion in the number of concepts available at the molecular level of analysis, especially in terms of distinct genes. Where earlier (and some contemporary) explanations from comparative embryology, morphology, and paleontology focus on the termination of a developmental trajectory or the change in timing of growth or differentiation, developmental geneticists are able to bring forth the expression pattern and function of multiple genes (greater than twelve in the case of avian feathers), the total of which is added to on a routine basis.[200] Because molecular level entities can be investigated *as* evolutionary innovations and novelties (Long *et al.* 2003a), there is a tendency to simultaneously utilize them as causal and evidential concepts while gleaning explanatory principles from the study of their origination (Ganfornina and Sánchez 1999; Gerhart and Kirschner 1997, ch. 5). But conceptual clusters for molecular biology/genetics oriented explanations do not involve development because the entities, activities, properties, and processes do not have ontogenies. Therefore, in addition to the number of molecular level concepts introduced, a key difference between conceptual clusters past and present is the increasing discrepancy between the level of organization at which the explanatory target concept resides and that of the causal and evidential concepts utilized.

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[200] This aspect can be underestimated due to the use of candidate gene approaches (Palopoli and Patel 1996). A entirely new *cluster* of Hox genes specific to reproduction was recently discovered (MacLean *et al.* 2005).

6.2.5.2. The Source and Character of Conceptual Change

The identified differences in conceptual clusters allow us to discuss the source and character of the conceptual change occurring. The objects or phenomena referred to as evolutionary innovations and novelties have been highly stable over the past seventy years (and longer). Part of this stability is referential but is also reflected in a stability of sense or meaning. The concepts of EVOLUTIONARY INNOVATION or NOVELTY have not undergone an obvious or significant change in meaning. But we can observe differences in the members of the conceptual clusters between past and present explanations. In particular, a number of phenomena have been added to the extension of the concepts of EVOLUTIONARY INNOVATION and NOVELTY, most notably molecular entities such as genes. This difference correlates with the structure of developmental genetic explanations, which use these new concepts as causes and/or evidence. Availability of these phenomena arises from the emergence of molecular biology and genetics in recent decades. The introduction of new concepts alone is not as significant as their nature (level of organization focused upon) and use in causal and evidential roles in conceptual clusters with respect to the problem agenda of evolutionary innovation and novelty.

Although there is an identifiable equilibrium state in the conceptual clusters of comparative development/embryology, morphology, and paleontology, developmental genetic approaches to answering these old morphological problems regarding innovation and novelty have disrupted it. This disruption involves a substantial alteration in the kinds of concepts representing causes and evidence in explanations of innovation and novelty typically found in comparative embryology, morphology, and paleontology, past and present. It represents a form of conceptual change in the sense of alterations in the components of conceptual clusters. Conceptual change is occurring with respect to a problem agenda, specifically the causal and evidential concepts invoked as explanatory, *rather* than with respect to a theory or meaning of the explanatory target concept. Because of the implicit equating of conceptual and theoretical change in many philosophical studies of scientific change, and an interest in referential changes for explanatory target concepts, the kind of conceptual change identified here can go unnoticed. This study identified a novel notion of conceptual change (and stasis) directly relevant to ongoing biological research that has been largely overlooked and may have wider relevance to understanding scientific change in other areas of research.

This behavior of conceptual clusters over time is similar to a phenomena termed 'concept expansion', which refers to the transformation of conceptual meaning through the addition of new instances purported to fall under a concept (Buzaglo 2002). The concepts of EVOLUTIONARY INNOVATION and NOVELTY have had new referents added at lower levels of organization, such as genes, but the meaning of these concepts has *not* been transformed. Instead, the conceptual clusters deployed in explaining innovations and novelties have been altered. This alteration correlates with the addition of these new referents but the conceptual change occurs apart from the explanatory target concept itself. The causal and evidential concepts show this conceptual difference as their utilization opens up a large disparity between the level of organization being explained (*explanandum*) and the level of organization at which entities and activities do the explaining (*explanans*). This conceptual difference is traceable to larger trends in biological science like molecularization that emphasize these lower level entities and activities as explanatory.

We can summarize our analysis of conceptual clusters as follows. First, stability of the explanatory target concept's meaning is paralleled by change in the conceptual clusters surrounding the explanatory target concept. The source of this change is the addition of new *molecular* phenomena as causal and evidential concepts. These new phenomena are biased toward lower levels of organization and emerge from broader trends of molecularization in the life sciences over the past four decades (Morange 1998). Support for this is found in the conceptual clusters now identifiable for developmental genetics and molecular biology, and the continuing similarity (equilibrium state) among comparative development/embryology, functional morphology, and paleontology. Although conceptual clusters in different disciplinary approaches share a number of features, including a bias toward entity explanatory target concepts, the use of activities as causal concepts, and the use of properties and processes as evidential concepts, key differences remain, especially regarding which concepts are borrowed. The conceptual change identified concerns the disruption of this conceptual cluster equilibrium state by a shift in the causal and evidential concepts utilized in explanations of innovation and novelty. The theme of tackling old morphological problems with new molecular tools found in contemporary Evo-devo *reflects conceptual change*, discernable in conceptual cluster use. Evaluating the import of this change requires that we direct our attention back to the criteria of explanatory adequacy of the problem agenda of innovation and novelty.

6.2.6. Commentary on the Reconstruction of Conceptual Clusters

Several methodological issues accompany these conceptual cluster reconstructions and the analytical results. First, the conceptual clusters detailed are not the only possible way to reconstruct the conceptual context. At several points, certain more or less inclusive conceptual categories were selected. One difficult reconstructive choice for conceptual clusters is the ‘grain’ or degree of abstraction. I strived to keep the grain fine rather than coarse but this was not always achieved (e.g. epigenetics). The incongruity of grain means that comparative results should be treated with caution. Also, conceptual clusters are not interpretable without the erotetic narrative that precedes them; they do not ‘stand alone’ as *the* structure of the explanation though they do indicate some of its features.

Another major issue related to grain returns us to the systematics analogy for the phylogenetic approach to philosophy of science: character choice and scoring. Particular characters (concept type, concept role, and ownership) with corresponding character states (concept type = entity, activity, property, relation, process; concept role = explanatory target, causal, evidential, other component; ownership = owned, borrowed) could be debated. Specific scoring of concepts within a cluster could be disputed also, such as when deciding not to label something a process because it is not well characterized. Each of these methodological issues looms large when considering the results derived from the analysis, just as they do in contemporary systematics (Kitching *et al.* 1998; Minelli 1993).

Another relevant concern from systematics is taxonomic sampling. I have offered five historical and eleven contemporary reconstructions from the materials presented in earlier chapters. There remains an abundance of source materials from which to reconstruct more conceptual clusters. It might be argued that the most consistent strategy is to select one explanatory target concept to focus on both historically and in the present. This strategy has two difficulties. First, it would severely restrict the number of explanations to be analyzed. Our review of past and present literature with a variety of explanatory target concepts facilitated the identification of interesting themes that would not have emerged otherwise. Second, for a particular explanatory target concept, there is not equal representation among disciplinary approaches. Thus, we would have missed distinctive features of conceptual use in behavioral biology if only treating the tetrapod limb. Since phylogenetic reconstruction is most robust when many different taxa are included, the multiple examples of varying kinds used (with an emphasis on developmental genetics explanations) could be further supplemented.

Recognizing reasons to be methodologically cautious about reconstructing conceptual clusters should not detract from the probative character of this analysis. One reason for the success of contemporary phylogenetic reconstruction is that a number of different researchers have conjointly produced increasingly large databases and analyses that have detected sensitivities in particular parameters of character choice, coding, and scoring. The reconstruction and analysis offered here is one among few (if not unique) and therefore cannot be expected to have identified these parameter sensitivities. Instead, the focus in our comparisons has been those features that appear to be robust. Conceptual change in the sense of conceptual cluster differences regarding the use of causal and evidentiary concepts from lower levels of organization to explain innovations and novelties is thus unlikely to be an artifact.

6.3. Consequences: Exploring Problem Agenda Criteria of Explanatory Adequacy

The discussion in Chapter 2 of the problem agenda of innovation and novelty involved two main aspects: individuation from other biological problem agendas and the characterization of its contours once individuated. The following sections draw out further ramifications of the criteria of explanatory adequacy for the problem agenda.

6.3.1. Individuation Consequences

One consequence of distinguishing the project of explaining innovations and novelties from other evolutionary questions is that natural selection is not an answer to the questions in this problem agenda. Selection is involved in the *preservation* and *diversification* of innovations and novelties but not their *origination*. This does not mean natural selection is not causally operating or that it is unimportant to the evolutionary history of species *containing* these innovations and novelties. Rather, the origin of variation at particular phylogenetic junctures requires an answer that is methodologically prior to any evaluation of particular selection pressures on individual characters or character suites. Paraphrasing Aristotle, these problem agendas are related but different because the causal processes collected under the term 'natural selection' that explain why variation was preserved at a particular phylogenetic juncture presuppose the answer to another problem ('why were those particular kinds of variation present at that phylogenetic juncture?'), which is explained by a nonequivalent set of causal processes.

This point can be emphasized through a previously articulated philosophical distinction between *actual sequence* explanations and *robust process* explanations (Jackson and Petit 1992; Sterelny 2001 [1996]; Sterelny and Griffiths 1999). Actual sequence explanations focus on the particulars of the causal history of entities under investigation to provide a satisfactory account of how an entity, state of affairs related to the entity, or modifications thereof came about ('what has happened in the actual world'). Robust process explanations on the other hand explain similar features by focusing on mechanisms that generate outcomes insensitive to vagaries in contextual conditions; i.e. an invocation of a robust process does not require attention to details of the causal history in order to be legitimate ('what would happen in many different possible worlds'). Natural selection explanations are exemplars of robust process type explanations. The clause 'at a particular phylogenetic juncture' is often absent when only considering natural selection. This modifier is required in the case of the origin of qualitatively new variation in evolutionary time. The problem agenda of innovation and novelty revolves around the issue of discrepancies between past and present states of variation and the uniqueness of particular phylogenetic junctures, which requires attention to actual sequence details. An explanation relevant to the problem agenda must attend to what has happened in the actual world rather than what might have happened in similar but different possible worlds. Therefore, an explanation of how variation originates developmentally in terms of a particular robust process (the origin of variation *in general*) is inadequate on its own to explain innovations and novelties (the origin of variation *at particular phylogenetic junctures*).

The distinction between actual sequence and robust process explanations was originally meant to explicate the nature of explanatory pluralism. Our individuation of the problem agenda of evolutionary innovation and novelty adds a further dynamic to this distinction for the case at hand. Robust process explanation components are compatible with actual sequence explanations of the origin of variation but the need for attention to *particular phylogenetic junctures* gives the actual sequence explanations *priority* in the overall explanatory project. Robust process type explanatory considerations will play a role (and in fact may be necessary) but they must be nested within an overarching actual sequence explanation. The actual sequence explanatory component contextualizes any robust process explanatory contributions. Although the robust process of *cis*-regulatory element modification leading to spatiotemporal changes in gene expression contributes to the origin of variation in general and was likely operative in the origin of multiple innovations and novelties, the explanatorily relevant aspect of *cis*-regulatory element modification for an innovation or novelty must be documented within the context of a particular phylogenetic juncture; e.g., a *cis*-regulatory element in *Hoxa2* of particular (now extinct) agnathan fishes was modified in an ancestral ontogeny leading to repression of *Hoxa2* gene expression, which allowed for the subsequent modification of the mandibular arches into gnathal elements. This issue emerges from the problem agenda being individuated in terms of particular phylogenetic junctures. Junctures pertaining to innovations and novelties are relatively rare, compared with those available in the history of life, and thus the invocation of robust processes involved in the origin of variation are not explanatory of the origin of innovations and novelties without further actual sequence explanation considerations.

Positively, the individuation of the problem agenda of innovation and novelty demands the inclusion of developmental biology because these kinds of causal processes are required to explain the existence of variation *per se* (cf. Wagner 2000). One cannot address the question of the origin of new variation without attention to the processes operating in animal and plant ontogeny. But an understanding of ontogeny cannot be reduced to the action and interaction of genes during development (cf. Love forthcoming; Oyama, Griffiths and Gray 2001; Robert 2004). A complete theory of phenotypic variation is required (Hallgrímmson 2003), which will include a variety of epigenetic processes and environmental factors that create, damp, exaggerate, or channel genetic variation in the ontogenetic production of a morphological feature (Müller and Newman 2003a; West-Eberhard 2003). Even if a skeptical position is adopted concerning the significance of epigenetics and phenotypic plasticity for the relationship between genotype and phenotype, the burden of proof lies with establishing their insignificance.

An objection might be raised to the seeming fact that only developmental genetic phenomena can be transmitted to the next generation. Besides the existence of a variety of heritable non-genetic factors affecting the phenotypic outcomes of developmental systems (Jablonka 2002; Oyama, Griffiths and Gray 2001), this objection amounts to changing the subject. Why variation was *heritable* at a particular phylogenetic juncture is a different question than why it was *possible* at the particular phylogenetic juncture. It is difficult to assess the heritability of variation without first knowing the nature of the variation. There can only be a privileging of developmental genetic explanations for the origin of novel features if there is a way to privilege genetic material in its fidelity of transmission and phenotypic effects during development. Neither premise is empirically supported at this time (cf. Love forthcoming; Oyama, Griffiths and Gray 2001; Robert 2004).

Our individuation result also implies that even though phylogenetic questions belong to their own distinct problem agenda (classification), it is necessary to utilize answers to these questions in order to adequately address the origin of qualitatively new variation. We can return to Aristotle and recognize that the question why particular kinds of variation were present at a phylogenetic juncture has embedded in it a different question regarding the determination of a particular phylogenetic juncture, which requires different answers than those for the origin of innovations and novelties. This embedding highlights the dual aspect nature of explanations of innovation and novelty. Adequately addressing the criteria of explanatory adequacy for the problem agenda requires recognizing the relevant embedded problems.

6.3.2. Characterization Consequences

A variety of results obtained by characterizing the problem agenda of innovation and novelty along three dimensions (form/novelty versus function/innovation; level of biological hierarchy in focus; and, degree of generalization available) are just as significant as the consequences derived from its individuation.

6.3.2.1. Form versus Function

The most noticeable consequence for this dimension is terminological. The term ‘innovation’ should be reserved for the origin of new functions and the term ‘novelty’ should be applied to the origin of new forms. In addition to clarifying scientific discourse, this has the advantage of reiterating the need for an account of the origin of particular *characters* that are complexes of form and function. Explicit attention to the origin of characters as form/function complexes largely remains an unfulfilled goal in contemporary research. Both INNOVATION and NOVELTY need to be kept separate from KEY INNOVATION, because natural selection is no longer a background condition for the latter concept. The intellectual habit of morphologists and paleontologists to move back and forth between origination and diversification is a direct site of application for this distinction. Again, this does not imply that the selectively advantageous consequences of having a novel feature in a particular lineage are unimportant. The diversification and maintenance of a particular feature is a different problem from the origin of particular kinds of variation at distinct phylogenetic junctures.

These terminological distinctions highlight biases in studies of form and function (cf. Chapter 3). Developmental genetic studies tend to focus on form and it is generally the case that most studies of developmental processes concern how form is produced (or constrained). There has been little study of the ontogeny of function *per se* for a variety of reasons, not least of which is the difficulty of studying the performance of organismal activities in fixed embryos or sections. But the ontogeny of function is causally significant with respect to the production of form, as seen in the dramatic effect of embryonic motility on bone and cartilage formation (Müller 2003a). We especially lack accounts of the ontogenetic production of function at higher levels of organization, in part because procedural hierarchies are often more difficult to dissect than compositional ones and function features are composed of multiple form features. Our impoverished comprehension of the ontogeny of function impairs an overall understanding of how innovations and novelties arise because without the functional component there can be no account of the origin of *characters* (form/function complexes) that play biological roles and bequeath selective advantages to lineages of organisms.

6.3.2.2. Level of Organization and Hierarchy

One fallacy confronting developmental researchers approaching evolutionary questions about character origination is translating compositional or procedural hierarchies in space into compositional or procedural hierarchies in time. The sequence of changes, whether genetic or epigenetic, that occurred at different levels of an ontogenetic hierarchy in evolutionary time to produce a phenotypic novelty may be quite different from the sequence of mechanistic changes observed in the ontogeny of an organism in developmental time (cf. Stern 2000). This is not identical to 'ontogeny recapitulates phylogeny' and researchers committing this fallacy explicitly reject recapitulation (e.g. Davidson, E.H. 2001). The problem is a kind of uniformitarian assumption that causal sequences now observed in ontogeny were also operating during ontogeny in the past. Besides the molecular paradox, which makes this assumption problematic, epigenetic explanations of body plan origin argue that the causal sequences producing form in the past operated much differently than those observed today (Newman 2003; Newman and Müller 2000). Arguments from phenotypic plasticity such as genetic assimilation imply that genetic changes now involved in the production of phenotypes have been added subsequent to the original production of the phenotype by environmental effects on ontogeny (West-Eberhard 2003; cf. Budd 1999).

This fallacy also feeds into a problematic conceptualization of causality that is sometimes adopted biologists working at the intersection of evolution and development. If it is assumed that causal sequences have always operated in the manner observed in present experimental analysis, and this analysis has a preferred set of investigative tools that are largely located at a particular hierarchical level, then the causal sequences scrutinized and used to explain the origin of variation will be those residing at or near that level of organization. If the means of investigation (such as molecular developmental genetic tools) are at a lower level of organization, far removed from the phenomena being explained (as is the case for most evolutionary innovations and novelties), then levels of organization become collapsed. Causal sequences at intervening levels of organization are ignored. Several examples of this were documented at the outset of Chapter 5.[201] Research from other levels of organization highlights the problematic nature of this conceptualization of developmental causation.

A final difficulty that attends this disparity between levels of organization is the possibility that self-organization type processes might produce form at higher levels of organization (Kauffman 1993; Kirschner, Gerhart and Mitchison 2000; Steinberg 2003). The origin of phenotypic variation due to these processes will not be elucidated through attention to lower hierarchical levels, such as gene expression, because there is no genuine compositional hierarchy to dissect. Conceptualizing self-organization processes *as* procedural hierarchies that produce form offers an alternative perspective on this possibility. Researchers interested in the origin of social insect behavior (i.e. function) have already pursued a similar line of reasoning (e.g. Beshers and Fewell 2001; Fewell 2003; Gordon 2001; Mitchell 2002; 2003, ch. 3).

The bias toward form features at lower levels of organization is pervasive in developmental genetic approaches to innovation and novelty. The form bias is also present in other disciplinary approaches, representing the relative inaccessibility of functional data from the

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[201] E.g., "Evolutionary change in the form of body parts requires evolutionary change in the gene regulatory network that controls pattern formation processes … For anyone interested in mechanism, there is in fact *no other way to conceive of* the basis of evolutionary change in bilaterian form than by change in the underlying developmental gene regulatory networks" (Davidson, E. H. 2001, 157, 201, my emphasis).

past in contrast to fossilized hard parts. Reductionist research heuristics have biases toward form over function and lower rather than higher levels of organization (Wimsatt 1980a, 1986; cf. Bechtel and Richardson 1993). Developmental genetic approaches exemplify a reductionist research heuristic because of the *combined* bias of form rather than function and lower rather than higher levels of organization. This interpretation is reinforced by another aspect of reductionist research strategies (cf. Section 1.4.1): the decision to individuate the system under analysis from its environment and understand its behavior in terms of the parts internal to the system. The user of reductionist research heuristics is biased in the choice of simplifying assumptions, executing necessary idealizations on the environment first rather than the system itself. Therefore the absence of phenotypic plasticity studies *within* developmental genetic explanations of innovation and novelty is another indicator of a reductionist research heuristic.

Morphologists and paleontologists have recognized this reductionist bias (Conway Morris 1994, 2000), but specification of the criteria of explanatory adequacy allows us to be precise about how the bias is operating. Developmental genetic explanations of innovation and novelty show three reductionist research heuristic biases: a preference for form over function, a focus on lower rather than higher levels of organization, and the simplification of environmental causal factors in favor of isolating causal import from intrasystemic components. The analysis of historical and contemporary explanations of innovation and novelty show that the preference for explaining form rather than function is not by itself indicative of a reductionist research heuristic, but arises from the nature of the data available for past phylogenetic junctures. In different language (Bechtel and Richardson 1993), developmental genetic explanations of innovation and novelty assume that *current* developmental system activities alone are relevant to the production of variation at particular phylogenetic junctures and pertinent causal factors can be localized in different system components (genes) or the interaction of these components (gene networks). The nature of the molecular paradox problematizes a *solitary* strategy of decomposition and localization of current developmental system components (genes) and their interactions (gene networks) for explaining innovations and novelties.

6.3.2.3. Generalization

Consideration of model organisms is central to evaluating the scope and power of explanations of innovation and novelty.

> We can carry out experiments ... under controlled conditions (in the laboratory, green house, or field), but the results will be highly dependent on which particular species, populations, and genotypes we have chosen. ... This means that not only the study of model systems, but the study of any particular group of organisms, will not likely yield results that can be generalized beyond fairly narrow taxonomic or life-history categories (Pigliucci 2004, 169).[202]

But the difficulties go beyond whether results gleaned from a particular model organism are representative of other organisms (Bolker 1995; Burian 1993a; Hedges 2002; Kellogg and Shaffer 1993; Schaffner 1998b). The issue of generalization for the problem agenda of innovation and novelty is focused along two specific trajectories. The first is how close model organisms are to the phylogenetic juncture. Studying mammalian jaw development in a murine system can yield powerful results but its distance from the proto-gnathostome common ancestor is great. Even for zebrafish there is 400 million years of evolutionary derivation since the origin of jaws (cf. Bolker 1995; Metscher and Ahlberg 1999).

Second, and related to the first, how well do the experimental systems approximate the ancestral variation capability of the species at the phylogenetic juncture (Wagner 2001b)?

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[202] At the genetic level, several surprises about the assumed genetic complement in the cnidarian-bilaterian common ancestral developmental system have recently been revealed (Kortschak *et al.* 2003). Model organisms such as *Caenorhabditis* and *Drosophila* have experienced major gene loss not previously recognized.

> Even using model taxa to investigate the origin of common, basic features can be problematic. This stems from the fact that most data have been amassed on mammals and birds, the two most recently evolved classes (and perhaps the most anatomically specialized). Extrapolating primarily from these taxa to important early events in vertebrate evolution (origin of the head, evolution of jaws), offers at best poor resolution of evolutionary sequences and their functional correlates (Hanken 1993, 449).

The specific populations of organisms that gave rise to variation bearing on many innovations and novelties are extinct. Modeling the ancestral variation capability requires knowledge of the rules governing the relationship between genotype and phenotype. Although these are unknown, they are likely applicable across most of evolutionary history (at least within metazoa). Another strategy for modeling this ancestral variation capability is to reconstruct a hypothetical developmental common ancestor using shared, plesiomorphic developmental characters derived from cladistic analysis (Northcutt 1990). This requires dense taxonomic sampling, which is at odds with the basic strategy of using model organisms in developmental investigation.

These concerns in combination with the molecular paradox produce a further dilemma.[203] An experimental organism may model a particular hierarchical level in other organisms quite accurately while simultaneously being a poor model for other levels. Generality across taxa for a particular hierarchical level does not result in generality across taxa, across hierarchical levels. The choice of model systems *for* developmental genetic investigation may be in conflict with investigating the origin of an innovation or novelty resulting from complicated procedural or compositional hierarchies. Although the choice of experimental organism matters (Burian

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[203] Molecular paradox = forms, functions, and characters at 'low' levels of compositional and procedural hierarchies (gene expression or protein complexes) generalize widely across a diversity of taxa whereas forms, functions, and characters at 'high' levels of compositional and procedural hierarchies (jaws or the tetrapod limb) generalize weakly because of the heterogeneity of possibilities (dissociation, co-option, epigenetics, self-organization) involved in producing the higher level of organization hierarchically (Genotype → Phenotype Map is Many → One). The molecular paradox and its consequences capture something distinct from the resistance among paleontologists about the extrapolation from microevolutionary processes to macroevolutionary patterns (Erwin 2000; Jablonski 2000), since the source of the latter is evolutionary processes above the species level such as species selection (Damuth and Heisler 1988; Gould 2002; Lloyd and Gould 1993; Sterelny 2001 [1996]; Vrba 1989).

1993a), there is not necessarily a best choice because of the need to model the appropriate *ancestral* variation. Historically, a broadly comparative approach utilizing dense taxonomic sampling also correlated with analyses at different levels of organization (Churchill 1997). Reflections on these matters motivate Evo-devo researchers to advocate integrated explanations derived from multidisciplinary research: "My main conclusion is that resolution of many fundamental and long-standing problems ... will require a combined approach that incorporates the technical and conceptual strengths of each discipline" (Hanken 1993, 448). How to achieve this combination is taken up in Section 6.4.

If we juxtapose the difficulty of modeling the ancestral variation capability of a species, using existing experimental organisms with the demand for an actual sequence explanation, a rigorous epistemological stricture emerges for explanations of evolutionary innovations and novelties. If the probability of transition from one phenotypic state to another (no jaws to jaws) is generally low and was only high at a particular phylogenetic juncture (early Ordovician agnathan fishes), then using extant taxa that exhibit developmental systems incapable of generating this variation on either side of the morphological transition (agnathans [lampreys] and gnathostomes [chick, mouse, and zebrafish] for vertebrate jaws) leaves it potentially impossible to causally demonstrate the morphological transition (Wagner 2001b). Even though developmental biology is necessary for explaining evolutionary novelties (Wagner 2000; Wagner, Chiu and Laubichler 2000), a relevant system generating variation germane to the origin of the novel feature may be unavailable for analysis. Especially vexing in this regard is character polarity for the gene expression patterns reviewed. For example, is the ancestral gene expression pattern for *Hoxa2* in the first branchial arch off or on? If it is the former, then the restriction of *Hoxa2* to the hyoid arch (and more caudal arches) *no longer plays a part* in the developmental genetic explanation of the origin of jaws.

Another issue under the dimension of generalization is the degree to which principles elucidated for innovations and novelties at a particular level of organization apply to other levels of organization. Some researchers argue that principles gleaned from one level apply to others: "…we will focus primarily on the gene level and discuss the evolutionary mechanisms that generate novelty, …we believe that the principles and mechanisms are applicable to any of the organizational levels" (Ganfornina and Sánchez 1999). Generalizations from molecular level analyses are widely applicable at commensurate levels but do not necessarily translate to higher levels, whereas the application of biomechanical principles can be generalized at these higher levels of organization. Gene duplication and divergence has received much attention and represents 'parcellation': modules are subdivided through the reduction of pleiotropic effects between units and/or augmentation of effects within particular units (Wagner 1996). The opposite process is 'integration' (Wagner 1996): two or more modules become a single unit by increasing pleiotropic interactions to establish new effects on previously independent characters. Whether parcellation is more common at the genetic level and/or other levels of organization has not yet been ascertained. The study of echinoid ectoderm territory differentiation empirically highlights this because it appears that an integration process has produced a single, novel embryonic territory from two previously distinct modules (Section 5.4; cf. Love and Raff forthcoming). The possible origin of extravestibular ectoderm through modular integration is a reminder that parcellation is not the only route to morphological diversity. Although evidence of duplication and divergence exists at the genic level, caution needs to be taken when principles gleaned from one level of biological organization are applied to another. Extrapolation of principles from particular hierarchical levels to understand the origin of evolutionary novelties at another level should be calibrated with solid empirical support at the level of interest. For example, the integration of distinct skeletal modules is a common feature in the evolution of skull morphology in vertebrates (Hanken and Hall 1993).

The current vogue of developmental genetic explanations of innovation and novelty is also connected with a key sociological feature of contemporary biology that antagonizes the difficulties associated with the molecular paradox. The number of biological researchers in disciplines primarily utilizing molecular data is dramatically larger than for other organizational levels (a ‘sociological corollary’ to the molecular paradox). Thus, it is not just that molecular data generalizes most consistently at the same level of biological hierarchy, far from that of interest for many innovations and novelties, but there is also a qualitatively larger amount of data at the molecular level that is being directed at features from higher levels of organization. Additionally, obtaining data related to the origin of form is usually easier and in more abundance than data concerning function, regardless of the level of organization in view (Lauder 1990).

Because generality across taxa for particular hierarchical level does not equal generality across taxa, across hierarchical levels, multidisciplinarity is required to achieve conceptual resources for form and function at all levels of the biological hierarchy with sufficient generality. Developmental genetic approaches to explaining the origin of novel features utilized in isolation will necessarily be deficient, and deficient to the degree of disparity between the genetic level and the level of organization exhibited by the particular innovation or novelty under scrutiny. Studies of gene expression, regulation, duplication and/or protein function can be generalized widely for understanding innovations and novelties at commensurate hierarchical levels but will be less informative for disparate hierarchical levels where many of the ‘traditional’ innovations and novelties reside. When this is conjoined with the sociological corollary to the molecular paradox, it becomes especially important to have disciplines that keep function in focus (functional morphology and behavioral biology) and that operate at high levels of structural organization (morphology and paleontology), as well as disciplines that contribute to the assessment of particular phylogenetic junctures and ancestral states of variation (phylogenetic systematics and paleontology). Because theory tends to follow data in biological sciences, the volume of data at lower hierarchical levels can skew attention to mechanisms and principles that are prevalent at those levels (cf. Ganfornina and Sánchez 1999). If the non-transitivity of molecular generalizations is forgotten, it may be difficult to maintain a multidisciplinary explanatory effort because the materials for generating a satisfactory explanation are not being equally investigated. This tension is exactly the kind of difficulty that a research area such as Evo-devo must confront (see below). The advantage of the preceding analysis is that it makes the criteria of explanatory adequacy explicit across the different required disciplines, serves to guide methodological choices for the contributions and interactions among these disciplines, and provides theoretical resources for achieving a multidisciplinary synthesis with respect to central item on the research agenda: explaining innovations and novelties.

6.3.3. Commentary on Developmental Genetic Explanations

6.3.3.1. Case Study Specific: Origin of Vertebrate Jaws

The features of the criteria of explanatory adequacy identified abstractly for the problem agenda of innovation and novelty are applicable to concrete research, such as developmental genetic explanations of vertebrate jaw origins (Section 5.3). These explanations are not the last word on the topic but incompleteness is not their only salient feature. The heterogeneity of developmental genetic results is a reminder that most of the genes discussed operate in pathways or feedback networks. Little attention has been paid to providing an integrated genetic pathway or network type explanation for the origin of jaws. In part this is a function of ignorance concerning relevant *cis*-regulatory elements and their modification. Attempts to identify the modification of existing regulatory elements for genes involved in vertebrate head and jaw development have not thus far yielded explanatory differences. Only conservation has been identified for *Dlx* regulatory elements (Sumiyama *et al.* 2002; Sumiyama and Ruddle 2003), and *cis*-regulatory elements of *Otx2* are conserved between mouse and pufferfish (Kimura *et al.* 1997). There is no evidence of *cis*-regulatory differences from cephalochordates/urochordates or agnathans to shed light on head or jaw origins, respectively.[204] Initial studies of gene regulation in lampreys show conservation of regulatory elements for actin genes expressed in skeletal and cardiac muscles, although the program for branchial and cranial muscles may be distinct (Kusakabe, Tochinai and Kuratani 2003).

There is no specific regulatory gene (or even a few taken together) whose altered expression in space or time is sufficient to explain jaw origins, though some reviews have tended to paint a picture along these lines (Graham 2002; Manzanares and Nieto 2003). The nested expression of *Dlx* alone cannot account for jaw origins because this pattern establishes proximal-distal orientation in *all* of the branchial arches. It is not clear whether the absence of *Hoxa2* in the first branchial arch is ancestral or derived, but if derived it does not explain any proximal-distal differentiation within the first branchial arch nor will it account for the elaborative divergence of morphology in the first branchial arch. Other genes share similar difficulties, such as *bapx1* and *noggin*, since joint formation occurs in *all* of the pharyngeal arches (though

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[204] Studies of gene regulation in amphioxus with respect to neural tube *Hox* gene expression point towards the possibility that new regulatory elements were required for the origin of vertebrate anterior features related to the head (Manzanares *et al.* 2000), but their existence has not been confirmed.

potentially ‘more critically’ in the first). Many of the genes discussed have not been subject to equally intense study and so their role in the origin of jaws remains obscure.

Any adequate developmental genetic explanation of an evolutionary novelty is complex because it involves detailing regulatory element changes leading to the co-option and/or modification after duplication for upwards of a dozen genes (not counting downstream structural genes) that are ‘wired’ into a network of interactions in an actual sequence type explanation. Should upstream components be considered initiators or followers in the origin of novel morphological structures? FGF8 and BMP4 operate very high in the regulatory cascades. Did alterations of their expression represent necessary first steps toward evolving a jaw apparatus or were they later altered to solidify the developmental outcome that had been tentatively established either by altered downstream structural or regulatory gene expression patterns (Chipman 2001) or epigenetic type interactions (Newman 2003; cf. Budd 1999)? This question relates to the relevant procedural hierarchy in evolutionary time underlying the origin of variation at this phylogenetic juncture and highlights the need to not commit the fallacy of assuming that causal sequences observed in present ontogenies operated equivalently in the ontogenies of the past.

Whether factors generating variation relevant to understanding the origin of an innovation or novelty primarily involve changes in gene expression or epigenetic dynamics is contentious (Davidson, E. H. 2001; Hinman *et al.* 2003; Newman 2003; Newman and Müller 2000). Developmental genetic changes are not causally sufficient to bring about phenotypic variation but many researchers assume they are. Necessity and sufficiency of causal power is contingent on genetic background, expression of other genes, and epigenetic interactions. Johnson has aptly noted that “the major skeletal gene is a unit of convenience produced by the skeletal geneticist" and that we need to be wary of genetic modifiers, genetic background (including the use of inbred strains), and pleiotropic effects (Johnson 1993), something which obtains for all of the 'jaw genes' discussed. These concerns are not often observed in the literature on jaw development and evolution.[205] Plesiomorphic pleiotropies need to be identified to interpret developmental genetic differences in craniofacial ontogeny, which requires a denser phylogenetic sampling of species studied. Compounding these difficulties, it is not always straightforward to discern when a gene mutation is having its developmental affect, and whether one is observing multiple effects across ontogenetic stages (Francis-West *et al.* 1998).

One outstanding feature of developmental genetic studies of jaw origins is their inattention to the ontogeny of function. This follows in part from investigating early patterning events when disruptions of gene expression do not yield functional morphology. But data from functional morphological studies on the ontogeny of jaw usage (e.g. Erickson, Lappin and Vliet 2003), especially the role of epigenetic and functional influences during skull growth (Herring 1993), and studies of later developmental stages such as life history transitions (Reilly 1994; Rose and Reiss 1993), need to be combined with developmental genetic investigations in order to address the origin of both form and function variation at higher levels of organization. Tracking large-scale functional patterns in the evolution of feeding systems is also relevant (Sanderson and Wassersug 1993). Much of the study of epigenetic and functional dynamics in skull growth and differentiation has been executed using mammals. Exceptional studies of various fish taxa need to take an explicitly developmental genetic turn, building on the existing data concerning life history stages (Ferry-Graham and Lauder 2001; Ferry-Graham, Wainwright and Bellwood 2001; Lauder and Shaffer 1993).

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[205] "What the *Dlx5/6* double knockout mice are telling us is that, at least at certain stages of mouth development, the only difference between upper and lower jaw is the expression of *Dlx5* and *Dlx6* and that both parts of the jaw share a largely common genetic program" (Manzanares and Nieto 2003, 898).

Finally, the derived nature of model systems being investigated needs to be considered. This is critical for gene expression in ammocete larvae of lampreys. If the larval form of lampreys is a derived condition, and the evidence is equivocal (Kuratani, Kuraku and Murakami 2002), then many gene expression comparisons would be suspect. Developmental genetic approaches to understanding the craniofacial elements that compose the jaw apparatus come from a small number of experimental systems: chick, mouse, and zebrafish. These species often exhibit highly derived features that are pragmatically useful in experimental analyzing them (Bolker 1995). They also are scattered taxonomically, without particular regard for the evolutionary histories of the characters and processes they are used to dissect, particularly with respect to cranial development and evolution (Hanken 1993; Metscher and Ahlberg 1999). Mouse, chick, and zebrafish studies are not a sufficient basis for generalizing to the molecular genetic architecture and developmental expression of a proto-gnathostome species so far removed phylogenetically. Additionally, the lack of taxonomic density in phylogenetic representations of model systems utilized in developmental genetic studies means that character polarities are often uncertain and similarities are interpreted primarily as conservation (not convergence), assuming a particular ancestral character state (Metscher and Ahlberg 1999).

Studies of lamprey species address some of these concerns but the lack of resolution for agnathan phylogenetic positions and potentially derived state of many lamprey characters is sobering. One uncontroversial consequence of remembering the issue of model organisms is to caution against overly quick generalization. For example, we cannot yet say that ‘lampreys’ have four *Dlx* genes (Graham 2002) because this was only found for *Petromyzon marinus*, while in *Lampetra japonica* only one cognate has been isolated. This is reinforced by the discrepancy in gene number for *Otx* between *Petromyzon* and *Lampetra*. Also, the phrase ‘in all gnathostomes' should be avoided: "all gnathostomes display nested expression of the *Dlx* gene pairs" (Graham 2002, R812). This is an unwarranted generalization (it is not even clear that all gnathostomes have each *Dlx* gene pair) and the appropriate clade based on these experimental organisms (mice, chick, and zebrafish) is osteichthys rather than gnathostome.

6.3.3.2. General Remarks

Since other developmental genetic explanations of innovation and novelty harbor these issues,[206] they can be treated more generally. An actual sequence type explanation requires detailing the actual molecular and developmental divergence, their effects through a compositional or procedural hierarchy on phenotypic structure or function, and the temporal sequence of its occurrence. Organisms near the relevant phylogenetic juncture may be unavailable for experimental investigation, making inferences *to* that particular phylogenetic juncture less solid. It is not sufficient to demonstrate that there is ontogenetic potential available to produce variation at the phylogenetic juncture in the form of co-option of existing genes or recruitment of paralogues through *cis*-regulatory region binding site changes. These mechanisms are available for any regulatory gene and establishing that one specific kind of regulatory change was critical for a key morphological transition (in a particular temporal sequence of change, coordinated with the evolution occurring in other genes belonging to the genetic network) is quite difficult.

The problem is not a difficulty in conceptualizing changes in genotype-phenotype mapping relations. Rather, there is *too much* developmental potential available in the logical space of regulatory evolution possibilities. Providing an actual sequence explanation of the

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[206] The model organism issue also arises for developmental genetic explanations of feather origination. *Gallus gallus* is a highly derived animal and its feather patterning and morphogenesis may not be representative of basal avian taxa that would best approximate the newly originated phenotype at the phylogenetic juncture in focus.

origin of jaws, or any other novelty, becomes elusive. Reasoning from actuality (observed innovation or novelty at a phenotypic level) backwards to *a* specifically responsible possibility (observed effect of an alteration in molecular genetic expression due to regulatory region alterations) is extremely difficult when the available contrast class of possibilities that *could be* responsible for (or, causally contribute) to a phenotypic outcome is large. This is a reversal of the strategy utilized for current studies of the generation of variation during ontogeny—from one or few possibilities to an actuality. The inferential structure pertaining to the problem agenda of innovation and novelty is the opposite—from an actuality to one of a multitude of possibilities. The dilemma is not only inherent in developmental genetic explanations; it arises whenever there is a disparity between the level of organization where the potential is being assessed and the level of organization where the actuality resides. It is arguably most exaggerated for developmental genetics due to the degree of discrepancy between levels of organization.[207]

Other disciplinary approaches are also deficient with respect to the three dimensions of the problem agenda of innovation and novelty. But they are not always deficient in the same respect. Behavioral biology keeps function very much in view alongside form but does not always attend to lower levels of the relevant procedural or compositional hierarchies.[208] Paleontology sometimes ignores lower levels of organization but focuses on form as primary because of inherent limitations with its historical source of data. An outcome of tracking the alternate approaches to innovation and novelty and reconstructing their conceptual clusters is the identification of conceptual heterogeneity with respect to the criteria of explanatory adequacy for

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[207] Practitioners of Evo-devo have also recognized this dilemma in the midst of technical advances in the establishment of both the pattern and process aspect of the problem agenda: "the field is still lacking effective ways to decide which [Evo-devo] scenario actually supports the developmental mechanisms responsible for an evolutionary character transformation" (Wagner and Larsson 2003, 2). This issue is also recognizable in Moss's discussion of the distinction between Gene-P (Phenotype Related) and Gene-D (Developmental Resource) concepts (Moss 2003). Gene-D reasoning of developmental researchers (from a set of possibilities to an actuality) does not mesh with Gene-P reasoning (from an actuality back to one of a multitude of possibilities).

[208] Endocrinology studies of behavioral innovation would be an exception.

the problem agenda. The pros and cons of this heterogeneity for each disciplinary approach direct us back to the necessity of multidisciplinary explanations of innovation and novelty in the context of Evo-devo *qua* disciplinary synthesis.

6.4. Evaluation: Evo-devo and Explaining Evolutionary Innovation and Novelty

6.4.1. The Nature of Evo-devo and Multidisciplinary Explanatory Demands

We are now in a position to evaluate the claims made with respect to the ability of an Evo-devo research program to offer solutions to longstanding problems concerning the origin of evolutionary innovations and novelties (e.g. Wagner, Chiu and Laubichler 2000; see Chapter 1). The results of our analysis of conceptual clusters and the problem agenda of innovation and novelty permit an evaluation of these claims from a conceptual standpoint; i.e., whether the epistemic framework of contemporary research is poised to offer satisfactory explanations of the problem agenda components.

But first another question must be asked: what exactly is the disciplinary composition of Evo-devo? In a recent review of an edited volume, McLaughlin captures a key difficulty in describing the research constitutive of Evo-devo.

> Although the themes of evolution and development are inherent in all of the contributions, the presentations are highly individualistic, even to the implied interpretation of evo-devo. To some of the authors, evolutionary developmental biology appears to relate to the broad interface of evolution and ontogeny, while others, evo-devo seems to be applied strictly to the use of molecular genetic data to analyze developmental observations. In the Introduction, the latter restriction initially is suggested; however, in the course of his discussion on ontogeny, evolutionary patterns and processes, Scholtz expands his concept of evo-devo to include all avenues of research from gene expressions to morphogenesis. Clearly, the definition of evo-devo, like other "buzzwords", is in the mind of the user (McLaughlin 2004, 279-280).

This tension is real, observable by contrasting Hall's description of Evo-devo as a multidisciplinary synthesis and Arthur's review of the state of Evo-devo: "…evolutionary developmental biology, or 'evo-devo' is focused on the developmental genetic machinery that lies behind embryological phenotypes" (Arthur 2002, 757).

But this tension, of which one side is reinforced by histories of exclusion that equate embryology with experimental embryology and ignore morphological and paleontological disciplines (Love 2003a, 2005; Love and Raff 2003; Raff and Love 2004; Chapter 4), can be *prescriptively* resolved from the standpoint of our analysis. Given that the criteria of explanatory adequacy for the problem agenda of innovation and novelty requires attention to form, function, and characters at all levels of the biological hierarchy with sufficient generality and that the molecular paradox prevents simplistic inferences from lower levels of organization (where developmental genetics operates) to higher levels of organization (where many innovations and novelties are situated), a phylogenetically situated developmental genetics is explanatorily inadequate. If Evo-devo is *not* a multidisciplinary synthesis then it is in a conceptually impoverished position to fulfill the promise of providing genuinely satisfactory explanations for the origin of novel features in the history of life. GENETIC PATHWAY or NETWORK cannot be the central organizing concept for Evo-devo (cf. Wilkins 2002) if it aims to explain innovation and novelty. The positive trend of using candidate genes to explore gene expression and function in a greater range of taxa (Palopoli and Patel 1996), i.e. increased density of taxon sampling, will be helpful and informative at lower levels of organization but, in principle, cannot fully address the question of how innovations and novelties arose at higher levels of organization.

From these considerations, Evo-devo must be a synthesis of different disciplines: "understanding and synthesizing this diversity *demands* a truly integrative approach and increased communication among the traditionally separate fields of genetics, molecular biology, developmental biology, paleontology, phylogenetics, morphology, and ecology (to name a few)" (Hall 1999a, xv, my emphasis). Some proponents recognize the need for an active synthesizing of these different approaches but realize it has yet to happen.

> The ultimate success of [Evo-devo], however, will depend on a synthesis of these disparate methodological standards …[Evo-devo] is still in a stage where the contributing disciplines are in conceptual *discontinuity* (Wagner and Larsson 2003, 1).
>
> If Evo-devo is to come of age, its different component approaches need to become more closely intertwined, both with each other and with relevant strands of other disciplines (Arthur 2004, 288).

The production of integrated explanations from multiple disciplines with conceptual resources for both form and function at all levels of biological hierarchy with sufficient generality to explain innovation and novelty has not yet occurred. Disciplinary heterogeneity within Evo-devo is an interesting phenomenon of study in itself. The communication between these different disciplines is highly variable and the numerical representation of researchers in each field is skewed towards those investigating molecular biological mechanisms, including genetics.[209] Methodological differences in the utilization and assessment of evidence and explanatory preferences must be addressed (Wagner and Larsson 2003); i.e., issues of non-semantic incommensurability are relevant to accomplishing the disciplinary synthesis.

How a genuine 'disciplinary synthesis' would look, operate, or if it can be sustained long enough to fulfill empirical promissory notes with respect to evolutionary innovations and novelties is therefore an open question. A prescriptive resolution in favor of a genuine disciplinary synthesis does not necessarily match the descriptive situation. Even if Evo-devo is not *just* comparative, molecular developmental genetics, research trends regarding the amount

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[209] Recall the sociological corollary to the molecular paradox described above (Section 6.3.2.3).

and type of data available increasingly means that it effectively *is* (cf. Baguñà and Garcia-Fernàndez 2003). Analyses of character origination will likely remain biased toward lower levels of organization, form rather than function, and the activities of entities internal to developmental systems rather than external environmental factors. These trends tend to discourage the multidisciplinarity needed to understand dynamics at higher levels of organization where many high profile novelties and innovations are situated. A number of researchers recognized this possibility fifteen years ago warning that "evolutionary developmental biology should not be reduced to the functioning of genes" (Wake *et al.* 1991, 588). Despite these concerns, Evo-devo has largely flourished in a molecular developmental genetic mode. Another suite of disciplinary separations may lie in the future, despite the advent of so many departments of 'integrative biology' aiming to offer a 'truly integrative approach'.

Maintaining a truly integrated approach requires a common commitment to a set of biological problems regardless of the current tools available to investigative those problems. Agreement on the nature of these problems is also necessary. Specification of the problem agenda of innovation and novelty provides a more precise statement of *why* different disciplinary approaches need to be synthesized into integrated explanations to satisfy the criteria of adequacy identified in its individuation and characterization. One of these dimensions, form versus function, isolates an explicitly articulated gap in the conceptualization of Evo-devo. In the inaugural issue of *Evolution & Development*, the editors opined that, "we seek nothing less than an integrated science of biological form" (Raff, R.A. *et al.* 1999, 2). Something more than an 'integrated science of biological form' is required to deal with the problem agenda of innovation and novelty; namely, an integrated science of biological form *and* function. But in addition to the fact *that* a disciplinary synthesis is needed, it remains to be seen *how* to produce integrated explanations from different disciplinary approaches using conceptual clusters in conjunction with these explanatory demands.

6.4.2. Normative Recommendations – Integrated Explanations

How can Evo-devo researchers keep the full explanatory demands of explaining innovation and novelty in view when faced with these very real tensions? How is the synthesizing of multiple disciplines with 'incommensurable' methodologies and criteria of explanatory adequacy accomplished in order to produce integrated explanations? The first step is a shared *acceptance* of the problem agenda of innovation and novelty, with its three primary criteria of explanatory adequacy and their joint consequences. But a common commitment to a problem agenda's structure and explanatory burden is only part of the task. The actual offering of explanations and prosecution of ongoing research requires the integrated deployment of conceptual resources from the different disciplinary approaches that adequately address the criteria of explanatory adequacy. To accomplish this the ideal of a *maximal* conceptual cluster can be introduced, where 'maximal' refers to the conceptual cluster being composed of all the requisite conceptual context members needed (at least as can be discerned now in ongoing research) in order to generate empirical results that will lead to a satisfactory solution. When coupled with the procedural connections among the different disciplinary approaches identified in this and previous chapters, a strategy for achieving a truly integrative approach can be produced.

Instead of representing the ideal of a maximal conceptual cluster with the format used for conceptual clusters, I adopt a different, indirect format, which captures some but not all of the requisite features required for a maximal conceptual cluster (Figure 9). The features represented are: (i) the different aspects of the explanation (pattern and process), (ii) the different disciplinary approaches, and (iii) the level of organization that these are most conceptually suited to address. The dimension of generality is indirectly captured by (iii) because soundness of generalizations correlates naturally with the level of organization addressed from within a disciplinary approach. Form versus function is not represented in the tabular format, which is actually biased toward form features under the levels of organization heading, but applies equally to the considerations outlined. Although disciplinary approaches play roles at particular levels of organization, they do not necessarily play the *same* role at that level of organization, which reflects the methodological differences inherent to each disciplinary nexus. But they broadly address either the pattern or the process component at commensurate levels of organization.

<table>
<tr><td></td><td>PATTERN</td><td>PROCESS</td><td rowspan="2">Level of Organization</td></tr>
<tr><td>Explanation Description</td><td><i>Non-homology</i>
<i>Phylogenetic Juncture</i></td><td><i>Mechanistic Account of Variation</i></td></tr>
<tr><td rowspan="3">Disciplinary Approaches</td><td rowspan="2">Paleontology/Morphology
Comparative Development
Systematics (Morphological)</td><td>Behavioral Biology
Quantitative Genetics
Functional Morphology</td><td rowspan="2"><i>HIGHER</i>
PHENOTYPE
PARTS
ORGANS
TISSUES</td></tr>
<tr><td>Epigenetics
Phenotypic Plasticity</td></tr>
<tr><td>Systematics (Molecular)
Developmental Genetics</td><td>Quantitative Genetics
Developmental Genetics
Molecular Biol./Genetics</td><td><i>LOWER</i>
CELL
GENETIC
BIOCHEMICAL</td></tr>
</table>

Figure 9: Disciplinary Contributions to Integrated Explanations of Innovation and Novelty

This representation highlights some of the natural disciplinary groupings identified throughout this study. The coordination of comparative embryology, morphology, paleontology, as well as systematics, is observable in the establishment of the pattern aspect at higher levels of organization. The grouping of behavior-phenotypic plasticity-epigenetics-functional morphology is also recognizable in the process component at middle to higher levels of organization. Other groupings, such as paleontology-ecology/environment, are not recovered because they reflect the conflation of origination and diversification. The environment invoked by paleontological researchers concerns the conditions of diversification and operation of natural selection ('key innovation') rather than the origins of the variation itself.

Another feature of this multi-dimensional representation of the conceptual resources needed to explain evolutionary innovation and novelty is that the conceptualization of phenomena at higher levels of organization resides with the disciplines that were the natural home to studies of innovation and novelty through most of the 20th century (Chapter 4). This parallels the observation that these objects are referentially stable and that developmental genetic explanations borrow their explanatory target concepts. The *explanandum* phenomena under scrutiny are conceptualized by *non-genetic* disciplines and therefore provide essential contours to the structure of an adequate explanation (cf. Wagner and Larsson 2003). By implication, higher-level units, including the organism, have methodological priority over lower levels in character identification (Wagner and Laubichler 2001). The claim made in Chapter 2 that characters serve as theoretical units of integration for form and function features in the problem agenda of innovation and novelty is thus made more explicit. Disciplinary approaches focused at higher levels of organization not only make a contribution to the explanation of innovations and novelties but a foundational one, without which the disciplinary approaches at lower levels of organization are unable to address particular problem agenda phenomena.

Because the ideal of a maximal conceptual cluster requires a multidisciplinary explanatory framework that integrates the heterogeneity of concepts concerning form and function at different levels of organization across a wide range of taxa in particular procedural relations, a natural question arises concerning its stability. Can the ideal of a maximal conceptual cluster simultaneously serve as an equilibrium state? Although there are no 'in principle' reasons to answer negatively, there are two *pragmatic* reasons for skepticism. First, the sociological corollary to the molecular paradox puts an inherent tension in the multidisciplinary conceptual framework due to the amount of data arriving at lower hierarchical levels. Tensions of this kind have pulled disciplines apart in the past, such as in the case of genetics and embryology. They represent a methodological impulse in favor of gathering *more* data *per se*, rather than reflecting on what *kind* of data are actually needed to generate an adequate explanation. Researchers often lose sight of the original question as new questions arise from the application of these successful data gathering methods. Second, this tension is not generic but strikes at the core of the three dimensions of the problem agenda of innovation and novelty. Developmental genetic evidential bias in the explanatory structure of Evo-devo implies the neglect of innovation (function) over novelty (form) and the ignoring of higher levels of organization, as well as difficulties arising from generalizing experimental results from highly derived model organisms and the molecular paradox. The impact of these pragmatic factors requires qualification in light of other Evo-devo research aims (see below) but prospects for the maintenance of a disciplinary synthesis producing integrated explanations of evolutionary innovations and novelties are not good.

The accomplishment of this section is a model of the conceptual resources required in order to adequately address the problem agenda phenomena in terms of a ‘maximal conceptual cluster’. This maximal conceptual cluster is formulated from multiple conceptual clusters, sequentially deployed, and reflective of the criteria of explanatory adequacy.[210] Although the study of innovations and novelties is a central component of Evo-devo, it is not the only item on the research agenda (cf. Arthur 2002, 2004a; Baguñà and Garcia-Fernàndez 2003; Hall 1999a; Hall and Olsson 2003; Wagner, Chiu and Laubichler 2000). The shared acceptance of the criteria of explanatory adequacy for the problem agenda of innovation and novelty may not be sufficient to maintain Evo-devo as a disciplinary synthesis. Clarifying the structure of these other research agenda items, individuating them from other problem agendas, and making explicit the criteria of explanatory adequacy needs to be executed. The overall strategy offered here does not immediately deal with issues inherent to these other phenomena without appropriate modulations. Research trends identified in the previous section indicate that if discrepancies in levels of organization exist, these other domains will be similarly affected. Therefore, this multidisciplinary explanatory strategy using the units of conceptual clusters and problem agendas may be profitable for other research items in Evo-devo.

6.4.3. Explanatory Pluralism and Interdisciplinary Epistemology

The model of integrated explanations from different disciplinary approaches for the problem agenda of innovation and novelty allows us to revisit the issue of explanatory pluralism and competition in explanations of biological phenomena. We observed in Section 6.3 that the distinction between robust process and actual sequence explanations is useful for specifying the

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[210] Evo-devo biologists recognize an expectation to produce these explanations. “Ultimately the success of a discipline depends on its ability to deliver on the promise the practitioners saw when the field was introduced” (Wagner and Larsson 2003, 1).

relationship among mutually compatible explanations in some domains but captures a key *difference* among explanation types relevant for the problem agenda of evolutionary innovation and novelty. The operation of natural selection upon heritable, fitness affecting variation deals with a different question than that of how the variation arises, especially at particular phylogenetic junctures. Individuating problem agendas identifies possible explanations that cannot be in competition because they answer related but different core questions determined by theoretical constraints. Discerning the nature of theoretical constraints (and presuppositions) extant in the biological sciences is thus extremely critical.

The idea of integrated explanations produced from a synthesis of disciplines builds on earlier philosophical work concerning the role of models and explanatory pluralism in biology. Biologists have long used a version of Tinbergen's 'four questions' pertaining to a behavioral trait as a framework for understanding the relationship among different explanations of similar biological phenomena (Tinbergen 1963): (1) What is the evolutionary history of a particular trait? (2) What is the current use of the particular trait in the life of the organism? (3) How does the particular trait develop over the life of the organism? and, (4) What mechanisms control the use of the particular trait? The problem with this framework is that it does not account for how explanations within particular questions might be competing or complementary. This issue has been treated by utilizing multiple false models to build a robust account of biological phenomena through reliance on the intersection of the 'false' simplifying assumptions inherent to the individual models (Wimsatt 1987; cf. Mitchell 2002). A related difficulty is that Tinbergen's framework interpreted as 'levels of analysis' is also deficient. Questions at different levels of analysis can compete because of interactions among causal processes at multiple levels of organization (Mitchell 1992; Mitchell 2002). The case of division of labor in social insects shows how explanations at different levels of analysis compete and explanations within a level can be complementary (Mitchell 1992; Mitchell 2002).

The explanatory framework from the previous section speaks to the issue of compatibilism and competition in three specific ways. One way concerns the individuation of problem agendas and picks out an appropriate contrast class of answers (via particular theoretical constraints and presuppositions) that can then be evaluated as to whether they are necessary or sufficient to explain the suite of phenomena under scrutiny. Individuation of the problem agenda excludes certain answers from the contrast class and therefore marks out where competition should not be occurring. The individuation is important not just in setting aside explanations relevant to other problem agendas but in making clear the relations among them. Natural selection explanations require the existence of variation and thus a natural selection explanation is not available if it is shown that variation does not exist in the developmental system (see Section 6.5.2, below). Problem agendas are not just different but exhibit ordered relations.[211]

The second contribution parallels Mitchell's arguments against the 'levels of analysis' formulation of Tinbergen's four questions (Mitchell 1992; Mitchell 2002). When attempting to give a mechanistic account of the origins of variation at a particular phylogenetic juncture, different causal mechanisms can be in competition at different levels of organization as a result of specific interactions occurring during ontogeny. (There is competition among members of the contrast class of answers.) The instance we have repeatedly returned to is the explanation of variation in terms of gene expression or gene networks versus appeals to epigenetics, self-organization, or external environmental factors impinging on developmental systems. These

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[211] This differs from Mitchell's interpretation of the conflict between selection and self-organization explanations for division of labor (Mitchell 1992; Mitchell 2002). She argues that they could come into conflict if self-organization processes indicate that no variation was available for selection to operate upon. I do not interpret this as conflict but rather as a consequence of the ordered relation among the problems.

different accounts can be in competition over accounting for the mechanistic origins of variation. They can also be considered complementary by combining them akin to Wimsatt's false model analysis (Wimsatt 1987) or Mitchell's integrative pluralism (Mitchell 2002), which emphasize relative frequency of occurrence and causal magnitude rather than mutual exclusivity.

The third area of application is in the dual aspect (pattern *and* process) nature of explanations of innovation and novelty. (This dual aspect can be understood as an ordered relation within a particular problem agenda, as opposed to an ordered relation between problem agendas as described above.) Competition does not arise between the aspects even when there is ample competition within an aspect. Therefore we can isolate another way in which explanations are competing or complementary. Although there is potential for explanatory competition about the causal factors responsible for the origin of variation ('process') and contention surrounds the establishment of homology and delineation of phylogenetic junctures ('pattern'), the evaluation of pattern and process are decoupled. For example, *compatibility* among explanatory components at the pattern aspect from different levels of organization, such as the relationships among taxa relevant to a phylogenetic juncture as determined by a molecular data set in systematics and known fossil finds in paleontology, could be accompanied by *competition* among levels of organization for the process component, such as the origin of variation as determined through *cis*-regulatory modification of regulatory genes from developmental genetics or via exogenous hormones from phenotypic plasticity studies.

Each of these outcomes bearing on the issue of explanatory pluralism is also relevant to interdisciplinary epistemology (Broido 1979; Kockelmans 1979a). For this study they identify when the different contributing disciplines of Evo-devo are in competition or offering (potentially) compatible explanatory components with respect to the problem agenda of evolutionary innovation and novelty. This can be put into the larger context of integration in interdisciplinary scientific endeavors (Bechtel 1986a; Bunge 2003; Mitchell *et al.* 1997; cf. Klein 1990, 1996; Kline 1995). One taxonomy of different integrating models identifies three broad strategies: mechanical rules, global and local unifications, and explanatory, concrete integration (Mitchell *et al.* 1997; cf. Mitchell 1992). Mechanical rules such as vector addition are most familiar from physics but have also been applied in biology. Global unifications attempt to generate unified theoretical structures that encompass all aspects of complex causal processes. Local or 'modest' unifications attempt to unite multiple aspects of these causal processes through increasing the realism regarding simplifying assumptions made when representing them. Explanatory, concrete integration concerns the unique combination and contribution of causal factors responsible for a particular phenomenon. The integrated, explanatory strategy offered here is a combination of modest unification and explanatory, concrete integration. It is similar to explanatory, concrete integration in the sense of attempting to account for the origin of particular innovations and novelties but also involves a modest unification because the integrative strategy applies to all of the phenomena within the problem agenda and affects the explanatory strategies applied to other problem agendas. Integration takes place with respect to *explanations*, for particular phenomena, and *solutions*, for all of the phenomena, both of which are relative to a particular problem agenda and its criteria of explanatory adequacy. Disciplinary syntheses provide the context for integrated explanations but concern more than a single problem agenda.

The significance of this analysis for interdisciplinary epistemology takes on greater value because Evo-devo is not the only putative multidisciplinary synthesis available.

> A unique combination of disciplines is emerging — evolutionary and ecological functional genomics — which focuses on the genes that affect ecological success and evolutionary fitness in natural environments and populations. Already this approach has

> provided insights that were not available from its disciplinary components in isolation (Feder and Mitchell-Olds 2003, 649).

The rationale offered by these authors for a multidisciplinary synthesis mirrors the one argued for in this study. "Because the mechanisms of each trait of interest are manifested at lower levels of biological organization and the significance of a trait is only apparent at higher levels, understanding a given trait usually requires the simultaneous use of molecular, cellular, organismal, population and ecological approaches" (Feder and Mitchell-Olds 2003, 649). Arguably, interdisciplinary interactions are becoming more common precisely because of a desire to bridge different levels of organization. A conceptual strategy for navigating competing and complementary components of participatory disciplines is available in my analysis.

Although I have not formally distinguished the adjectives 'multidisciplinary' and 'interdisciplinary', some have argued that the former refers to research that brings disciplines together while retaining their distinctness whereas the latter integrates multiple disciplines to produce a common outcome (Beggs 1999; Collins 2002; cf. Klein 1990, 1996; Kline 1995).[212] Multidisciplinarity tends to be transient while interdisciplinarity often leads to the formation of a new discipline thereby establishing a more permanent juxtaposition. The kind of explanatory strategy advocated in the previous section is interdisciplinary according to this definition. Evo-devo is often referred to as a distinct 'discipline' (Hall 1999a; Raff 2000), and there are institutional reasons to consider it as such (professional societies, new research journals, dedicated funding, textbooks, and specified job openings) (Lenoir 1997; Klein 1990; Kline 1995; Messer-Davidow, Shumway and Sylvan 1993). But it seems better characterized as a cross-disciplinary research cluster (Bechtel 1986b, 1993; cf. Kockelmans 1979a) akin to

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[212] Beggs, following Kockelmans (Kockelmans 1979a), makes a variety of further distinctions, such as *pluridisciplinary* (research involving multiple but already related disciplines) (Beggs 1999; cf. Klein 1990, ch. 3). It is not clear that these distinctions are helpful beyond the more basic separation of multidisciplinary and interdisciplinary.

‘interdisciplinary’ *sensu* Beggs rather than as a new discipline. The integrated explanations being offered for innovations and novelties consist of multiple contributions from different existing disciplines to a common problem *agenda* without researchers having to abandon their extant disciplinary identity. Therefore, the ‘interdisciplinary’ character of the explanatory strategy does not demand a single, united discipline for its execution. Evo-devo *qua* new discipline is understood as the sociological condition for fulfilling the epistemological condition of Evo-devo *qua* disciplinary synthesis in order to produce integrated explanations that address the criteria of explanatory adequacy.

My analysis also has consequences for how ‘interdisciplinary’ work should be understood by funding agencies. Because the disciplinary synthesis is directed at a problem agenda involving multiple investigative questions of different kinds rather than a single problem pertaining to only one particular theory or model, a corresponding recognition of explanatory difficulty needs to be acknowledged. Grants awarded in three to five years cycles will always be useful but it is unlikely that a problem agenda will be adequately addressed in that amount of time (cf. Klein 1990, ch. 8; Kline 1995). The stability of problem agendas indicates that the disciplinary syntheses required to deal with them need to be maintained for much longer periods of time than usually conceived. Consequently, the impact of the sociological corollary to the molecular paradox also should be considered for longer time scales. This bolsters the pessimism that a maximal conceptual cluster can be maintained by a disciplinary synthesis as an equilibrium state for a sufficient period of time to generate sufficient empirical results that allow the criteria of explanatory adequacy for the problem agenda to be adequately addressed.

6.5. Implications: Neo-Darwinism and Evolutionary Theory

6.5.1. The Structure and Adequacy of Evolutionary Theory

Another major question relevant to this study is whether the specification of the problem agenda of innovation and novelty in the context of Evo-devo is a complement or challenge to neo-Darwinism. We broached the topic in Chapter 2 by distinguishing the problem agenda of innovation and novelty rather than subsuming it underneath the problem agenda of adaptation within neo-Darwinism. Does this amount to a criticism of the explanatory sufficiency of neo-Darwinism and, if so, are we in need of a new or expanded evolutionary theory?

Early rhetoric in the 1980s surrounding the juxtaposition of evolution and development emphasized strong conflicts between developmental researchers and evolutionary theory (Goodwin 1984; Goodwin, Holder and Wylie 1983; Gould 1980b; Ho and Saunders 1984; Løvtrup 1987; Webster and Goodwin 1982), although others were more accommodating of a place for development within evolutionary theorizing (Grant 1985, ch. 33). Reactions were equally polarized (Mayr 1991; Wallace 1986), and a number of problematic arguments were evaluated and found wanting, whereas others were seen as open questions (Burian 1988; Futuyma 1988; Gayon 1990; Grene 1990). The query has continued to elicit variegated answers from Evo-devo proponents and other biologists (Arthur 2000a, 2004b; Atkinson 1992; Erwin 2000; Horder 1989; Leroi 2000; Müller 1991b; Müller and Newman 2003b), as well as philosophers (Amundson 2001; Burian 2005; Griffiths and Gray 1994, 2001, 2004; Robert 2004; Sterelny 2000; Walsh 2003). On my analysis, any evolutionary theory that does not include developmental biology will be unable to explain the origin of innovations or novelties (cf. Wagner 2000). This is derived from the existence of distinct problems that require attention to different sets of causal processes.[213] Evolutionary theory of the past sixty years, understood in terms of selection on populations of alleles with changes in their frequencies, is incomplete *because it assumed an answer to a problem it was not designed to explain*—the developmental connection between genotype and phenotype.

Focusing on the existence of different problem agendas does not controvert all of the results obtained within a neo-Darwinian framework. Rather than wholesale theoretical change, this constitutes a clarification of question domains in evolutionary theory and reminds us of the historical claim in Chapter 4 concerning the Modern Synthesis 'excluding' evolutionary studies at higher levels of organization. The theoretical patterns observed in the Modern Synthesis can be understood as codifying a particular set of questions as the domain of evolutionary theory, exclusive of a mechanistic account of the origin of variation.[214] A dual recognition of the *significance* of these neglected or 'other' problems and an appropriate clarification of their *distinctive* character and *difference* from other questions, as well as the *ordered relations* among the problems, situates Evo-devo as a primarily complimentary investigative framework concerning the origin of evolutionary innovations and novelties.

Adequately tackling the issue of reformulating evolutionary theory cannot be accomplished here. This requires an answer to very difficult questions such as 'is the synthetic theory of evolution really a theory?' and, if so, what is its structure, which draws us into questions on the nature of scientific theories. But we have developed tools and produced an analysis pertinent to these issues so a cursory answer is worth the attempt. Cursory answers should be cautious so mine are conditionally formulated and based on qualified descriptive

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[213] This can be described in different terms, such as whether the relations in the problem concern 'parts to wholes' or 'instances to kinds' (Gerson 2005) or whether explanations track quantities or objects (Griesemer 2005).

[214] There is a significant sociological dimension to the choice of problems and structure of research that emerged from the Modern Synthesis that must be ignored here (cf. Cain 1993; Gerson 1998, 2005; Smocovitis 1996).

categories. The qualified descriptions concern evolutionary theory *qua* neo-Darwinism. What do we include as the epistemic product of the Modern Synthesis that is being evaluated for explanatory sufficiency? Many have noted that the synthetic theory of evolution is not best construed as *a theory* but rather as something that played a supra-theoretical, organizing role (Burian 1988; Darden 1986; Gayon 1990), which was both epistemic and social (Beatty 1986; Smocovitis 1996). If we also consider a stricter interpretation of neo-Darwinism in terms of mathematical theory available for discussing changes in genetic features from generation to generation (i.e. evolutionary genetics), we have (at least) two ways of referring to evolutionary theory. *Strictly*, it is the behavior of gene frequencies in Mendelian populations according to the Hardy-Weinberg population equations with natural selection as the primary causal factor producing directed change in those frequencies and measurable at the phenotypic level with quantitative genetics (cf. Lloyd 1988). Adaptation and diversity are the central phenomena of interest, as catalogued by ecological researchers and systematists. *More broadly*, evolutionary theory is this core of evolutionary genetics with adaptation and diversity as the primary phenomena *plus* positive intellectual commitments (gradualism and the extrapolation of microevolution to macroevolution), negative intellectual commitments (*contra* essentialism, Lamarckian inheritance, orthogenesis, and saltation), and the collected results of different disciplines (e.g. paleontology), interpreted within this framework (Futuyma 1988; Gould 1983; Mayr 1959, 1980, 1993). This is observable in evolutionary biology textbooks where the major sections cover these domains *in this order*: evolutionary genetics, adaptation and natural selection, evolution and diversity (including biogeography, speciation, and systematics), and macroevolution (including paleobiology) (Ridley 1996, 2004).

Narrow and wide interpretations of 'evolutionary theory' thus constitute the antecedents of our two conditional assessments of potential implications. Evolutionary theory (*sensu stricto*) is not supposed to provide a theory of phenotypic variation, in the sense of offering a mechanistic account of how the variation that is heritable and exhibits fitness effects is ontogenetically generated. Distinguishing the problem agenda of innovation and novelty does not impugn evolutionary genetics but rather reveals a problem domain that is not formally addressed by it. Evolutionary theory (*sensu stricto*) need not be expanded because it does not concern this question. The difficulty with this view is that the connection between changes in genotype tracked by population genetics and phenotype tracked by quantitative genetics is mediated via development. If the genotype-phenotype map is *not* transparent in the sense of additive relationships between genotype changes and phenotype changes without significant contributions from epistatic interactions, environmental input, or epigenetic processes during ontogeny (cf. Walsh 2003), then the problem agenda of innovation and novelty focuses attention on developmental data that call into question the universal applicability of the requisite assumptions of evolutionary theory (*sensu stricto*).[215]

This lends some credence to a broader interpretation of evolutionary theory (*sensu lato*), which should provide a theory of phenotypic variation at particular phylogenetic junctures in order to be adequate in scope and force to account for the evolutionary history of life. Thus, distinguishing the problem agenda of innovation and novelty isolates a lacuna in neo-Darwinism that, if not addressed, leaves it explanatorily insufficient as an evolutionary theory (*sensu lato*). This does not invalidate the findings of much of the research referred to as evolutionary theory (*sensu stricto*). Rather, it advocates a broader domain of evolutionary explanatory targets that

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[215] Astute commentators have recognized this (cf. Burian 1988). This assumption was made by originators of the Modern Synthesis, such as R.A. Fisher (Grene 1961; Hodge 1992a; Morrison 2002).

are not encompassed by evolutionary genetics. The second conditional assessment is favorable because evolutionary theory is usually interpreted to include the intellectual commitments that find no place in the formal machinery of population and quantitative genetics (i.e., a *sensu lato* interpretation). But this simultaneously raises the issue of circumscribing evolutionary theory, which currently exists in a heterogeneous form with little to no agreement regarding its 'essential' structure (Gould 2002; cf. Arthur 2004b, Lloyd 1988). Opting for a *sensu lato* interpretation is more descriptively accurate but suffers from imprecision because it is achieved by relaxing what is (and is not) considered 'evolutionary theory'.

Summing up these considerations, if we understand evolutionary theory in the more limited sense, then it is not clear that it needs to be expanded to include the problem agenda of innovation and novelty but the issues surrounding the study of the genotype-phenotype map impinge on assumptions about the developmental connection between genotype and phenotype utilized in evolutionary genetics. Evolutionary theory may need to modify these assumptions but does not require fundamental retooling. If we understand evolutionary theory in the broader sense (i.e. as Neo-Darwinism), then the problem agenda of innovation and novelty should be included since it is currently not addressed within either the mathematical formalism *or* the intellectual commitments. But, consequently, what counts as evolutionary theory becomes unclear; it has lost its definite referential status.

Although we cannot adjudicate between these options here, because justifying either conditional (or another option) is far from trivial, our study of problem agendas suggests a potential solution that is favorable to the second conditional (evolutionary theory *sensu lato*). Evolutionary theory could be conceptualized as a set of problem agendas that are relevant to understanding the evolutionary history of organisms. Candidates would include adaptation, classification, innovation and novelty, and speciation. The relative stability of problem agendas is an important aspect of this conceptualization. Instead of asking what the structure of evolutionary theory is, the first step is to clarify the nature of the problems in need of explanation. One advantage of adopting the problem agenda as a unit of analysis is that it emphasizes the need to make criteria of explanatory adequacy explicit across different biological disciplines, which is highly relevant to the shaping of an evolutionary theory that recognizes methodological and substantive contributions from disciplines outside of evolutionary genetics.

Each of these problem agendas is related to one another but can be distinguished using existing theoretical constraints in biological science. Executing this is no small task, but it has the potential to capture the relative contributions of different disciplinary contributions to explanations of evolutionary phenomena and isolate the origin and nature of particular intellectual commitments. We have already observed how disciplinary contributions can be synthesized into integrated explanations of innovations and novelties. The bias of the Modern Synthesis against higher levels of organization often studied by developmentally oriented researchers, observable in the positive commitment to the extrapolation of microevolution (i.e. gene frequency changes) to macroevolution (i.e. major phenotypic change) and the negative commitment regarding saltation, arose from assumptions about the genotype-phenotype map. One can reconstruct this as the exclusion of a particular problem agenda, the mechanistic origin of variation at particular phylogenetic junctures. Understanding which problem agendas are considered part of evolutionary theory at a given period of history may illuminate the structure of evolutionary theory, as well as its evolution through time.

Admittedly, these are argument sketches requiring further substantiation. They are offered as future directions of research in light of the philosophical tools developed here (conceptual clusters and problem agendas). I have concentrated on the structure of evolutionary theory because it touches on one of the original questions of this study: what does it mean to say that explaining innovations and novelties is 'outside the scope' or 'explanatory range' of evolutionary theory? Although on either interpretation of evolutionary theory given above the answer is a qualified 'yes', the effect of these implications on what *should* be the explanatory range of evolutionary theory remain to be addressed.

6.5.2. Natural Selection, Revisited

Finally, we can revisit why distinguishing the problem agenda of innovation and novelty does not impugn the explanatory power of natural selection although it rules it out as an explanatory factor. Hodge has forcefully argued that the structure of Darwin's argument for natural selection was made with reference to the *vera causa* ideal articulated by Herschel, Whewell, and Mill (Hodge 1977, 1989, 1992b, 1992c, 2000). This led Darwin to argue in a stepwise fashion for the *existence* of natural selection as a causal process, its *adequacy* to produce, adapt and diversify species, and its *responsibility* for having produced the living and fossil species observed (Hodge 1977, 1992b). Many past discussions of innovation and novelty have been premised on the inability of natural selection to produce these phenotypic features, which can be construed as a criticism of the second step; natural selection is not adequate to produce these morphological changes. The individuation of the problem agenda of innovation and novelty achieved in this study in terms of the mechanistic origins of variation at particular phylogenetic junctures reveals *that the adequacy of natural selection is not in question*.

The *existence* of natural selection as a 'causal' process depends on the presence of variation that has differential fitness effects and is heritable. Thus, the conditions for the operation of natural selection presuppose the generation of variation, which is in part a concern of developmental biology. Natural selection cannot be deemed inadequate with respect to its causal power in the absence of variation. Its causal power is moot until the conditions for its operation are in place. It only makes sense to ask if natural selection is adequate and responsible if variation is available for natural selection to be in existence. (The dimension of phylogenetic juncture adds an additional criterion regarding discrepancies between past states of variation and those available for causal analysis by developmental biology in the present.)

This conclusion bears on recent discussions of the relationship between evolution and development by philosophers of biology. For example, Walsh has argued that natural selection theory and studies of development can be reconciled by abandoning the view that natural selection is a causal force (Walsh 2003; cf. Walsh 2000; Walsh, Lewens and Ariew 2002). Making natural selection merely a statistical aspect of varying populations rather than a causal force has been criticized (Stephens 2004), but my discussion reveals a different difficulty. Walsh maintains that the primary explanatory target of a combined theory of evolution and development is adaptedness and diversity but, as we have seen, the problem agenda of innovation and novelty does not concern these phenomena (as it does not aim to explain adaptive evolution). Similarly, attention to the issue of phylogenetic juncture is absent from Walsh's discussion, which reveals insensitivity to this constraint on theories of development whose goal is to explain the origin of variation when discrepancies exist between states of variation past and present. A theory of development in the sense of a mechanistic explanation of the developmental causes of phenotypic variation (e.g. the genotype-phenotype map) combined with natural selection theory is inadequate as a framework for evolutionary theory because it assumes that the probability of transition from one phenotypic state to another is not conditioned by the phylogenetic juncture under consideration.

6.6. Concluding Remarks on the Analysis

In Section 6.2 ('Interpretations and Comparisons') we reconstructed conceptual clusters with an erotetic narrative and a tabular representation format. Concepts were scored for their role (explanatory target, causal, evidential, and other), type (entity, activity, property, process, and relation), and ownership (borrowed versus owned). We compared similarities and differences in the conceptual clusters past and present. The structure of these explanations showed similarities in entities as explanatory target concepts, activities as causal concepts, and processes or properties as evidential concepts. An equilibrium state was identifiable for the conceptual clusters of comparative embryology, paleontology, and morphology, and contemporary developmental genetic explanations were distinctive in borrowing their explanatory target concept. The major 'conceptual change' identified was the shift toward and numerical increase in entities from lower levels of organization playing a role as causal and evidential concepts. This change occurred with respect to explanations of the problem agenda phenomena not with respect to the meaning of the concepts themselves. Methodological issues were flagged concerning the grain of conceptual clusters, character choice, and scoring, which emerge from our systematics analogy for the phylogenetic approach to philosophy of science.

Section 6.3 ('Consequences') revisited the problem agenda of innovation and novelty and the specific consequences arising from its individuation and characterization. The problem agenda of innovation and novelty is best understood as demanding an overall actual sequence explanation rather than a robust process explanation in virtue of the 'at a particular phylogenetic juncture' clause. A mechanistic explanation of the processes generating variation demands attention to more than gene expression and regulation. Characterization consequences for the problem agenda include: the terminological distinction between innovation and novelty; the recognition of inattention to the ontogeny of function at higher levels of organization; the identification of the fallacy of confusing hierarchies in developmental space with hierarchies in evolutionary time; the tendency to collapse levels of organization in the conceptualization of causality during ontogeny when there is large disparity between the putative causes and the phenomenon to be explained; the existence and operation of a reductionist research heuristic in developmental genetic explanations of innovation and novelty; the difficulty of using experimental models that are not near the relevant phylogenetic juncture; the difficulty of modeling the ancestral system of variation, including models being better suited for particular levels of organization; the potential impossibility of demonstrating the origin of variation at particular phylogenetic junctures in light of the actual sequence explanatory demand; the problems with assuming principles related to the origin of innovations and novelties are the same across hierarchical levels (parcellation versus integration); and, the sociological corollary to the molecular paradox with its asymmetry of data accumulation and biases toward lower levels of organization and form rather than function features. These consequences were identified in the vertebrate jaw origins case study and general aspects of developmental genetic explanations of innovation and novelty were elucidated, such as the dilemma of 'too much potential'.

In Section 6.4 ('Evaluation') we tackled whether Evo-devo is in a unique position to explain the origin of innovations and novelties. Although the structure of Evo-devo varies depending on who describes it, we prescriptively favored understanding it as a disciplinary synthesis because of the explanatory demand of the problem agenda of innovation and novelty.

This disciplinary synthesis is currently in ‘conceptual discontinuity’ but a model of integrated explanations of innovation and novelty was proposed that could in part serve as template for meshing the differences in methodology, explanatory standards, and aims of research within Evo-devo. The first aspect of this model was a shared acceptance of the criteria of explanatory adequacy for problem agenda. The second aspect involved the ideal of a maximal conceptual cluster that was represented through a format identifying how and where the conceptual resources of the different disciplinary approaches are required. Whether this maximal conceptual cluster could be maintained as an equilibrium state was answered pessimistically. These issues were then filtered through broader considerations on the nature of explanatory pluralism and interdisciplinary epistemology.

In Section 6.5 (‘Implications’) the results of our analysis were applied to the adequacy of evolutionary theory. Although its structure is open to multiple interpretations, the need for developmental considerations to be incorporated stands out. Conceptualizing evolutionary theory in terms of interrelated sets of problem agendas was suggested as an alternative perspective that allows a better understanding of the heterogeneity of ongoing evolutionary research and may be helpful in thinking about evolutionary theory historically. The causal efficacy of natural selection is not impugned since it does not exist in the absence of variation and therefore a mechanistic explanation of the origin of variation is a precondition for explaining its operation (a different but related problem). Attempts to reconcile evolution and development by claiming that natural selection is merely ‘statistical’ are unnecessary and unhelpful because they do not rightly characterize this fundamental difference in explanatory task.

7. Applicability of Investigative Methodology, Philosophical Testability, Outstanding Questions, and Summary

7.1. Introduction to the End

In this concluding chapter we step back from our historical and philosophical analysis of the problem agenda of innovation and novelty in order to ask whether the strategy adopted is only applicable in this very specialized area of biological science. The methodology of this study can be used in other domains, in part because of flexibility available in its application. One source of confidence in its potential applicability, whether in the life sciences or elsewhere, is that the procedure is a blend of previously vetted investigative strategies from historians and philosophers of science. I argue here that the *specific strategy of blending* adopted is amenable to other contexts (Section 7.2). In addition to general applicability, a second thematic question concerns the testability of this philosophical account. The danger of reading one's preferred philosophy of science into studies of scientific activity needs to be avoided (Hull 2001c; Maull 1976). Articulating my perspective on the 'testability' of conceptual clusters and problem agendas constitutes an important reflexive capstone (Section 7.3).

Section 7.4 identifies questions that go beyond what has been argued in previous chapters. There are several natural avenues of future research that emerge from this investigation that can be formulated as outstanding questions. The arguments in each of these three sections are not meant to be definitive. They serve to make connections with the wider philosophy of science community on several common points of interest. The chapter closes by rehearsing the entire argument of the dissertation with a chapter-by-chapter summary (Section 7.5). The main outline of the study is reiterated and the unique contributions are highlighted, providing a synoptic perspective from which to recall them.

7.2. General Applicability of the Methodology

In order to assess whether a phylogenetic approach to the philosophy of science is applicable to other domains, it is necessary to bring forward its basic structure (cf. Section 1.3.2).

i. A foundational problem is identified in a particular research area and carefully characterized.
ii. A concept (or several concepts) central to the scientific conceptualization of this problem is (are) chosen as the focal unit(s) for investigation.
iii. An analysis is undertaken of how these concepts are used in explanations concerning the focal problem in contemporary research.
iv. Historical investigation is undertaken over a selected period of time with respect to the focal concepts and problems.
v. Results from (iii) and (iv) are compared to identify interesting similarities and differences, the latter yielding a preliminary account of ‘conceptual change’.
vi. Results from (iii) are compared against the explanatory demands articulated in (i) to determine if the present explanations are positioned to address the problem.
vii. The identification of any mismatch between the explanatory aims derived from the nature of the problem and the current conceptual structure of attempted explanations leads to specific proposals for redressing this mismatch.
viii. Results are consulted to identify their broader impact on issues in philosophy of science.

The first steps of this methodology fit naturally with the questions that gave us our analytical units, concepts and problems, and animated the entire study: are there different problems in biological sciences and do explanations of innovations and novelties fall outside the scope of evolutionary theory? These units were further refined into *conceptual clusters* and *problem agendas*. Thus, 'how concepts are used in explanations' became more precise in the detailing of conceptual clusters and the 'characterization of the foundational problem' became the delineation of criteria of explanatory adequacy for the problem agenda.

How generally applicable is this methodology? This question can be answered with respect to particular sciences and with respect to whether the specific analytical units developed are utilized. If we first consider the basic methodological procedure, there seems little reason to restrict its application to life sciences alone. Whether physical, life, or social sciences, including their many sub-domains and disciplines, there are (and will be) foundational problems, concepts, and explanations to consider (cf. Suppes 1990). Some philosophers of science already utilize a methodology focusing on the use of concepts in explanations. But at step (iv) the differences begin to emerge. Many philosophical studies are unaware of the historical context of the concepts, problems, and explanations under scrutiny, without which the diachronic comparison in stage (v) cannot be made. Conceptual change is one area of research in philosophy of science where ahistorical approaches are notably hamstrung. This is especially significant for the later steps because our historical analysis contextualized our findings from present scientific practice, such as comparative embryology, morphology, and paleontology being the main loci of research on innovations and novelties and the increasing hierarchical gap between the *explanandum* and *explanans* observable in developmental genetic explanations. The historical analysis also impinged on our normative recommendations because it is not just the disparity of concepts at different levels of organization that is relevant but also their continually increasing number (sociological corollary to the molecular paradox) as a consequence of a broad trend in biological research over the past four decades (molecularization). These methodological considerations appear very relevant to physical and social sciences.

The situation is not as clear-cut when we consider the specific analytical units. Although there is no reason to think that other scientific domains do not utilize multiple concepts in the offering of explanations (conceptual clusters), the significance of these may not be similar to that observed in this study. Part of the significance of conceptual clusters is derived from the stability of meaning and reference for the explanatory target concept. Whether physical, social, or even other biological science explanatory target concepts display a similar stability is unclear apart from further investigation. The usefulness of problem agendas may be lessened because they are designed to describe the contours of this stability. Most accounts of problems in philosophy of science were forged on physical science examples. Physical science phenomena and the explanatory problems they pose seem prone to alteration when theoretical changes occur, unlike biological problem agenda phenomena. But it may be that parallels can be recovered, such as the motion of ‘terrestrial’ bodies rather than the motion of ‘heavenly’ bodies. It may even be that the motion of supraterrestrial objects can be understood as a problem agenda by parsing a difference in the effect of theory on *conceptualizing* the phenomena versus *explaining* the phenomena.

A different approach to comprehend how the methodology articulated and exemplified in the previous chapters might be applicable to other philosophical investigations of science is to highlight four broad components of any philosophy of science methodology.

- What phenomenological feature of scientific activity are you trying to explain/understand? I.e., what philosophy of science area will you focus upon?

- How will you operationalize this feature? I.e., how will you explicate it such that you are able to pick out relevant information and ignore other aspects of scientific practice?

- Where will you apply this operationalization? I.e., where will you take your more precise concerns derived from a philosophy of science perspective for actual investigation?

- What will you do with the results of your investigation? I.e., how will you direct your conclusions and to whom?

In my analysis, conceptual change or revision corresponds to the first component, especially with respect to the practice of offering scientific explanations. The second component was addressed in our account of conceptual change in terms of alterations in conceptual clusters and their equilibrium states. The third component involved the identification of a foundational problem (innovation and novelty), which was then explored both in the past and present via conceptual clusters for the different explanations offered. Finally, the results were directed to the scientific community of interest (Evo-devo) and philosophers of science interested in conceptual revision. Although these components are found in most philosophy of science endeavors, they are not necessarily made explicit. Weak points in investigative strategies sometimes lurk in implicit or unclear answers to these procedural questions.

The flexibility available in the methodology of this dissertation can be seen by way of illustration. Identical answers can be provided for the first two questions (concentrate on conceptual change and use the analytical units of conceptual clusters and problem agendas), as well as the focus on foundational problems, to explore a very different area of science (physical, life, or social science). Results can then be directed to the relevant audience, either philosophers, scientists, or both. Alternatively, the first question can receive a different answer. The philosophical domain of interest might be the structure of scientific theories or the relation between evidence and hypotheses. These would then need to be appropriately operationalized before being applied to a domain of science, foundational problem or otherwise. Similar strategies have been executed fruitfully in philosophy of science and my discussion of them here is possible because of this prior work.

One potentially contentious methodological feature was whether a philosophical investigation of this kind should make normative recommendations for scientific practice. I distinguished weak, moderate, and strong normativity in Section 1.3.3, opting for a form of moderate normativity, but this element need not have been included in the analysis. The results regarding conceptual change can be dissociated from those related to the criteria of explanatory adequacy in the problem agenda and contemporary explanations of innovation and novelty. Another dimension of normativity is the making of prescriptive recommendations for the philosophical literature (whether or not explicitly concerned with philosophy of science). This emerges when existing philosophical distinctions do not 'carve the joints' of scientific activity where they should. One reason for exploring the applicability of the methodology arises from the concern that the kind of conceptual change documented (conceptual cluster differences) has not received adequate attention from philosophers of science. Another is that many philosophers of mind and language have not focused on the joint deployment of concepts but rather their representational structure. Although this aspect of normativity has not been a primary focus of this study, I have adopted it more explicitly elsewhere (Love 2003b).

The range of flexibility available in the overall procedural sequence speaks to the utility of the methodology adopted in this investigation. Whether it is the kinds of questions that can be investigated, the different ways that operationalization can be executed, the freedom in selecting different sciences and domains to focus upon, and the ability but not requirement to make normative recommendations, application flexibility is a mark in its favor. But four features stand out in this flexibility and undergird a more specific imitation of the methodological procedure: the role of history, the use of foundational problems, the use of particular analytical units, and the value of drawing prescriptive in addition to descriptive conclusions. We have already addressed the role of history in philosophical investigation (above and Section 1.3.1) and the value of drawing normative conclusions (above and Section 1.3.3). The significance of conceptual clusters and problem agendas as analytical units is argued in Chapter 1 and 2, respectively. On all three counts, there are reasons to see them as essential to the outcome of this study and potentially relevant in other domains. For example, framing normative conclusions for scientists demands that the issues driving their conceptual difficulties are in focus rather than preconceived notions of what they should be worried about.

Turning to foundational problems *in the sciences*, there is a sharp contrast between analyses motivated by problems in the philosophical literature and those motivated by problems emerging from scientific investigation. One of the most distinctive contrasts is the reliance upon imaginary examples in the former and actual examples in the latter. Philosophical analysis executed on exotic fictionalized scenarios requires the problematic use of intuitions about these scenarios as evidence (cf. DePaul and Ramsey 1998; Hull 1989, 1997). The use of actual, detailed examples has been intentional in the present study because they provide the requisite detail apart from intuitions to execute this type of epistemological analysis. Another distinctive is that foundational problems within science are a locus of 'messy' thinking, providing an observer with interesting variations and conflicts in the thought of different researchers rather than the complete logical space of possibilities. This heterogeneity is not contrived, although it may be confused, and thus is more relevant to the epistemological study of science.

Reconstructions of a logical space of possibilities in philosophical analyses of science are sometimes insensitive to and unilluminating of the practice of science (cf. Rasmussen 2001).

These considerations constitute a rationale for the general applicability of the methodological procedure adopted herein, including the specific units of analysis. Arguably, the most poignant question to emerge from reviewing these reasons is whether the conceptual behavior described and documented in this study is a province of biological science alone or reflects deeper patterns in scientific reasoning (see below, Section 7.4).

7.3. Testing Philosophical Claims about Science

Establishing meta-scientific claims is difficult and theory-ladenness is arguably more of a problem for philosophers than for scientists (Hull 2001c; Maull 1976). Hull has noted four domains that require consideration: (1) idealization, (2) testing, (3) operationalization, and (4) normativity (Hull 2001c). We have already directly addressed two of these domains. Normativity was the subject of Section 1.3.3 (and above), where we located the specific prescriptive range of the analysis. Operationalization was discussed in Chapter 1 in terms of a conceptual cluster surrounding an explanatory target concept (illustrated in Chapter 6) and problem agendas were explicated on analogy with van Fraassen's account of explanation in terms of answers to why questions (Chapter 2). In this section I treat how my account of conceptual change is subject to some kind of testing, closing with a comment on idealization.

It has recently been argued that Hull has offered the best account of scientific change, at least with respect to biological science (Richards 2002). Hull's account is evolutionary, drawing on a selection based mechanism directly isomorphic to that used in evolutionary theory (Hull 1988a, 1988b). One of the bases for Richards' evaluation of Hull is a shared commitment to treating the philosophical claims about science as we would scientific claims themselves; i.e., as subject to judgment at an empirical tribunal (Hull 2001a, 2001b). But, drawing on our historiographic discussion (Section 1.3), evolutionary theories of scientific change need not be selection based to be subject to evidential considerations. Historical case studies can favor particular hypotheses about guiding assumptions and theory change that are not explicitly founded on selection mechanisms (Donovan *et al.* 1992 [1988]).

One reason a number of historians and philosophers have preferred selection mechanisms is because of the theoretical precision afforded when directly applying the scientific model of change to models of scientific change itself (Campbell 1974). But our distance from early modern natural philosophy reveals how uncomfortable we are with philosophical theorizing as *part of* scientific activity. The aims of philosophical theorizing are often probative and not subject to direct confirmation in the sense of applying some standardized statistical measure to data. A philosophical account of conceptual change in science can be evaluated empirically by whether it illuminates the practice of science even if it is difficult to 'formally' confirm (or disconfirm) it (cf. Suppes 1990). We broached this subject in our discussion of the phylogenetic approach to philosophy of science when labeling the strategy 'satisficing' or heuristic (in the sense of problem solving) rather than attempting to provide a general theory. The appropriate empirical test is not whether it applies to another area of science or even biology but how it helps in understanding the issues surrounding the problem agenda of innovation and novelty.

Another avenue to the subtlety of testing philosophical ideas is through the role of philosophical exegesis; the philosopher is an interpreter and generator of interpretations.

> Rarely does a philosophical thesis make its debut in a formulation clear and precise enough to admit adjudication. Before a verdict can be rendered on its merits, the thesis must be refined to the point where evaluation can take place. Not just any clear and

> precise rendition of the thesis will do. Unless the reconstructed thesis bears certain relationships to the original, evidence that bears on the former may fail to bear in the same way on the latter, … What these relationships must be depends on one's objectives, and in particular on whether one hopes to substantiate or to discredit the original thesis (Massey 1992, 317).

This issue of interpretation is salient with respect to testing because it emphasizes that the evaluation (empirical or otherwise) of a philosophical thesis is more nuanced than a crucial test between two hypotheses. These subtleties need to be incorporated into our picture of empirically evaluating philosophical perspectives on science. Drawing attention to different conceptualizations of testing philosophical ideas is not meant to insulate theorizing in philosophy of science from empirical refutation. Rather, it widens the space of confirmation beyond the battery of tools typically used in contemporary science and imagined when discussing empirical tests of philosophical claims about science. There is more than one way to empirically evaluate whether a thesis concerning conceptual change maps onto past and present scientific practices.

One way to achieve empirical precision for the present philosophical account is through attention to criteria of adequacy for a theory of conceptual change (or scientific change more generally). Burian has offered a set of constraints on a theory of conceptual change that are derived from difficulties attending 'autonomous' and 'historicist' analyses of science (Burian 1987). Autonomous analyses aim to establish scientific standards as a philosophical rather than scientific enterprise, executed by the use of particular philosophical techniques and then applied to scientific claims. Historicist analyses eschew establishing standards for science and instead attempt to describe scientific standards in use, clarify which standards are appropriate for given contextual scientific aims, and identify confusions from standards applied out of context. The six constraints or criteria of adequacy are (Burian 1987, 19):

a. An acceptable philosophical account of the phenomena of conceptual change ought to contain apparatus facilitating evaluation of the discontinuities exhibited by historical science – discontinuities in fundamental beliefs, evaluative standards and methodologies, systems of concepts, theories, and so on.
b. It should be prepared to evaluate those shifts-in-standards which, at least in the short run, permit reductions in the explanatory scope and competence of acceptable theories.
c. These evaluations should not be applicable only retrospectively; they should also be applicable to ongoing work in which the precise boundaries between theories and disciplines, and the precise content of particular theories, is not settled.
d. The philosopher's evaluative apparatus should not exclude, a priori, comparative evaluations … of the rival "conceptual schemes," "explanatory ideals," "paradigms," and so on pertinent to theoretical science.
e. It should not automatically exclude point-by-point comparison of the predictions of contemporaneous versions of rival theories belonging to rival research traditions.
f. If a theory of meaning is employed by the philosopher or built into his apparatus, it should not, by itself, exclude such point-by-point comparison.

The first three constraints are derived from difficulties attending autonomous analyses and the second set emerges from difficulties with historicist approaches. These constraints can be seen as responses to two basic desiderata for analyses of scientific change (Burian 1987, 26):

- The system for evaluating scientific work and scientific standards should not be chauvinist – that is, it should not automatically accept or approve as reasonable only those explanations, theories, standards, and values which are acceptable to some one scientific community or which incorporate only the commitments of some particular conceptual scheme.

- The system for evaluating science and scientific standards should be applicable to, and able to benefit from, detailed historical case studies of successful and unsuccessful science

The account set forth in this dissertation navigates these six constraints explicitly and is responsive more generally to these two desiderata.

The apparatus of conceptual clusters and problem agendas facilitates the evaluation of discontinuities in the history science, picking out key differences in what is in need of explanation, the criteria of explanatory adequacy, the methodologies involved, and 'systems' of concepts utilized. Conceptual clusters allow for a previously unrecognized form of conceptual change to be isolated that does not require meaning change in the explanatory target concept.

Conceptual clusters and problem agendas permit the evaluation of shifts in standards, either through change in conceptual cluster equilibrium states or the addition, deletion, and modification of questions within a problem agenda. Each of these is conducive to the observation of reductions in the explanatory scope and competence of acceptable theoretical frameworks. Conceptual clusters and problem agendas are “applicable to ongoing work in which the precise boundaries between theories and disciplines, and the precise content of particular theories, is not settled”. This was a central component of our study because of Evo-devo *qua* disciplinary synthesis. The ‘evaluative apparatus’ of conceptual clusters and problem agendas does not exclude comparative evaluations of alternative conceptual perspectives or disciplinary approaches. We identified explicit differences in explanatory ideals, such as the rejection of the presupposition for the problem agenda of evolutionary innovation and novelty by some evolutionary geneticists, and articulated a model for blending disciplinary approaches. Conceptual clusters and problem agendas do not preclude specific comparisons of predictions from rival explanatory frameworks of different disciplinary approaches. Potential conflicts between genetic and epigenetic accounts of variation were recognized, which facilitates more explicit evaluation of their relative merit with respect to one another. Finally, a specific theory of meaning was not built into the analytical units utilized and therefore also does not preclude these types of comparisons.

With respect to the dual desiderata given by Burian, the apparatus of conceptual clusters and problem agendas is not chauvinist. It does not merely approve explanations, theories, standards, or values of one scientific community or incorporate commitments only from one conceptual point of view. We rejected the rationale given by Evo-devo proponents for the distinctness of the problem of innovation and novelty, found the use of developmental genetic tools inadequate in isolation to supply satisfactory answers to questions about the origin of innovations and novelties, and identified the complementarity of contributions from different disciplinary approaches through a model of integrated explanations. My apparatus is also applicable to and benefits from detailed historical case studies of successful and unsuccessful scientific endeavors. These features are especially evident in the analysis of historical explanations of innovation and novelty in Chapter 4.

This project simultaneously involves an independently motivated account of conceptual change and the modulation of that account as it is employed in the particular case study at hand. "When philosophers of science deal with such context-specific issues, they tend to refine and differentiate their tools to suit the particular questions at hand" (Burian 1987, 28). Although this kind of strategy has been criticized on the basis of a lack of sampling and absence of rigorous statistical methods (Faust and Meehl 2002), it is not clear that these meta-scientific analyses touch directly on the microstructure of conceptual change. They also are committed to a unimodal perspective on empirical evaluation in terms of statistical significance. This perspective on testing philosophical theories derives from the desire to give an account for how all of science operates. The *heuristic* strategy advocated here (and by others) allows one to adopt a perspective on testing philosophical ideas in particular scientific contexts that involves multiple modes including statistical significance, problem solving effectiveness, and the meeting of explicit philosophical criteria of adequacy (constraints and desiderata).

In closing this section it is important to return to Hull's final issue involved in establishing meta-scientific claims: idealization. Conceptual clusters and problem agendas do not exhaust scientific practice. Many features of biological investigation and explanation are not captured in the analytical apparatus. The use of these philosophical tools and the claims regarding conceptual change derived from them represent an idealization, ignoring certain details while highlighting and modeling others (cf. Maull 1976). Idealizations are a necessary part of scientific activity and philosophical theorizing. The real concern is whether the idealization somehow significantly skews the outcome. For example, one could worry about the ignoring of sociological factors involved in concept use and the establishing of criteria of explanatory adequacy. But every research heuristic has a bias and can be made to fail (Wimsatt 1980a). Our goal is similar to that articulated for integrated explanations; the synthesis of many false or idealized models using different philosophical research heuristics as a means to a more robust picture of the nature of scientific practice (Mitchell 2002; Wimsatt 1987).

7.4. Outstanding Questions, Future Research

In any study of this kind a number of outstanding questions can be isolated and serve as points of departure for future research. Some of these pertain to more general philosophical issues whereas others arise from further exploration of the biological sciences analyzed in this study. Here I list some of these questions, grouping them as either historical or philosophical. For the latter, I distinguish questions pertinent to general philosophy and those relevant to philosophy of science or biology in particular.

7.4.1. Historical Questions

- *Does the application of conceptual clusters and problem agendas as analytic units to particular periods of the history of biology reveal continuities or discontinuities previously unrecognized?*

- *Does the issue of disparities in the levels of organization investigated for different disciplinary approaches in biological research allow for a more perspicacious reconstruction of developments in 20th century biology?*

- *Does the thesis regarding a 'hardening' of the Modern Synthesis require modification in light of the historical research on evolutionary innovations and novelties?*

- *Does looking for conceptual change in the sense of conceptual cluster alterations identify either conceptual changes in the midst of conceptual stability previously identified or conceptual cluster stability in the midst of conceptual instability previously identified?*

Doubtless, more historical questions could be discerned. The general thrust concerns what would happen if we used conceptual clusters and problem agendas, as well as some of the results from the analysis, to reevaluate particular claims about or patterns in the history of biology.

7.4.2. Philosophical Questions

7.4.2.1. General Philosophy

- *Can conceptual clusters be adequately supplemented with a theory of meaning using inferential or conceptual role semantics?*

- *Is the molecularism of scientific concepts relatively unique or are there more biases from the use of a reductionist research heuristic among certain philosophers of mind and language?*

- *Do the kinds of conceptual differences identified by conceptual clusters and problem agendas within disciplinary syntheses in science apply to conceptual differences among purportedly rational knowers in other domains?*

- *How does the account of conceptual clusters and problem agendas mesh, if at all, with existing epistemological debates such as internalism versus externalism about justification or how different forms of evidence (sense-perception, memory, testimony, and introspection) should be weighted and jointly integrated (if at all) in rational discourse?*

In section 1.2.5 we retreated from semantic interpretations of conceptual clusters in order to avoid controversies surrounding the semantics of concepts and whether concepts obtain meaning from their relationships with other concepts. Marrying conceptual clusters to a particular theory of meaning may be a fruitful strategy for identifying further aspects of conceptual change related to those identified here. The isolation of further reductionist research heuristic biases in philosophy of language and mind could address fundamental disagreements about methodology among philosophers. Interesting connections with traditional epistemological questions about justification and forms of evidence are possible, such as the ability to integrate different forms of evidence into jointly acceptable decisions among diverse rational agents, but a more thorough study is needed to substantiate any similarities or differences.

7.4.2.2. Philosophy of Science and Biology

- *Are there principled reasons to prefer pragmatic approaches to cognitive activity in science rather than symbolic/representationalist approaches?*

- *Can philosophy of science be divided into historical and ahistorical modes based on the investigative questions being asked?*

- *Can evolutionary theory be philosophically articulated in terms of relationally ordered problem agendas?*

- *Does the model of integrated explanations with multiple disciplinary contributions and shared criteria of explanatory adequacy apply to connections between life science disciplines and social science disciplines or life science disciplines and physical science disciplines?*

- *Do biological problem agendas other than evolutionary innovation and novelty have similar or different conceptual cluster behavior? Can these similarities and differences be correlated with the criteria of explanatory adequacy for the problem agenda?*

- *Are equilibrium states of conceptual clusters significant markers of conceptual stasis, often associated with the domain of 'normal science'?*

- *Are problem agendas applicable to physical science phenomena?*

- *Does the phylogenetic approach demand more than pattern? How far does agnosticism about mechanisms extend?*

- *Can we ever move from moderate normativity to strong normativity? Can we bridge the gap between explanatory standards for special sciences and values for all of science, or provide standards of scientific rationality?*

- *Does the notion of material inference or material relations among concepts bear on theories of scientific explanation?*

- *Can conceptual clusters and problem agendas be articulated in conjunction with a particular theory of explanation?*

- *Do debates about incommensurability need to be explicitly revisited with non-semantic issues in focus? Would this alter conclusions about the presence or significance of incommensurability in science?*

- *Does attention to the diversity of phenomena referred to as 'conceptual change' in philosophical studies of science imply that this category is problematic?*

Our focus on use rather than representation in Chapter 1 was driven by the recognition that many features of scientific practice are missed when a symbolic, representationalist approach to scientific knowledge structures is adopted. Since this has been a primary strategy in philosophy of science, the present study has value in identifying things previously overlooked regardless of whether this strategy should be preferred in all philosophical studies of science. Questions about the application of problem agendas to physical science were identified in Section 7.2 when considering the general applicability of the analytic tools. The stability of biological problem agendas may not hold for physical science problem agendas, which appear to have more theoretically constituted phenomena. If so, it could constitute a fundamental difference between physical and biological science that demands a pluralistic approach to philosophy of science. This would militate against an affirmative answer to whether we can ever move from moderate to strong normativity. These answers turn on whether problem agendas are found useful in examining other scientific (including biological) problem agendas. Affirmative answers to the problematic character of the notion of conceptual change and prior discussions of incommensurability would require significant reevaluation of case studies from the history of science used by philosophers of science. Conceptual clusters and problem agendas already intercalate with broadly causal theories of explanation but do not appear incompatible with other theory types such as unification. The role of material inference and material relations among concepts is naturally broached when discussing the *formal* structure of scientific explanation as inferential.

Again, other questions could be isolated, including queries about social factors in the articulation of disciplinary syntheses or conceptual cluster behavior. Many of these questions are not easily answered and require a major research investment. A distinctive feature of these questions is their emergence from the analysis, pointing toward historical and philosophical issues that have not received adequate treatment. The formulation of these questions is another result of this dissertation and their articulation significant prior to being formally addressed.

7.5. Dissertation Summary

7.5.1. Chapter 1

The subject of the dissertation is explanations of evolutionary innovations and novelties, especially as found and emphasized in the new research area of Evo-devo. Proponents of Evo-devo have made multiple claims about their potential as a synthesis of biological disciplines to offer explanations of innovations and novelties, which raise a number of historical and philosophical questions: ‘was the study of evolutionary innovations and novelties ignored over the past fifty years?’; ‘how does a synthesis of different biological disciplines navigate epistemological differences in goals, methodology, and criteria of explanatory adequacy?’; and ‘what does it mean to talk about different ‘problems’ in biological science?’. Two natural analytical units can be isolated from these questions, concepts and problems, and each is developed into a more specific unit, *conceptual clusters* and *problem agendas*, respectively. The overarching methodology utilized in developing these tools is to focus on scientific practice or the use of concepts. This dovetails with recent research on the role of natural kind concepts in the explanatory practice of scientists.

The primary insight concerning the conceptual practices of scientists is that concepts are always jointly deployed in the offering of explanations for particular phenomena. These 'clusters' of concepts pertain to the horizontal relationships among scientific concepts rather than vertical relationships obtaining between perceptual concepts and scientific concepts. Each cluster is anchored by a central explanatory target concept. In order to explicate the notion of a conceptual cluster, two metaphors are explored: toolkits and neighborhoods. The toolkit metaphor flags that the multiple concepts used by a disciplinary nexus can be either owned or borrowed and represent particular concept types (entity, activity, property, relation, process), similar to tool types. The neighborhood metaphor is employed to bring out the structure of conceptual clusters, which is methodologically analogous to emphasizing the material properties of concepts (their empirical content) rather than their formal relations. This structure of conceptual clusters is historically useful because it operationally picks out a kind of stability (conceptual cluster equilibrium states) and change in conceptual use, which differs from earlier philosophy of science endeavors. Part of this operationalization is accomplished through understanding the conceptual cluster as addressed to a problem agenda, as well as a noncommittal approach to the semantic ramifications of conceptual cluster changes.

Conceptual clusters pick out a form of conceptual change, which connects with broader issues in philosophy of science. Several considerations indicate that for particular philosophy of science problems such as conceptual change, a historical approach is necessary. But conceptual clusters are not an attempt to articulate a *theory of* conceptual change, unlike many previous investigative strategies in philosophy of science. Rather, the analytical unit is used heuristically to solve the problems arising in the particular context of Evo-devo (a satisficing strategy). There are several ways to understand the history needed to dissect conceptual change and the present study favors an evolutionary approach to science but focuses on the reconstruction of historical patterns rather than selection processes. This ‘phylogenetic approach to philosophy of science’ concentrates on the origin of contemporary problems in the past of science on analogy with phylogenetic reconstruction in systematics. The import of this strategy is not just descriptive but exhibits ‘moderate normativity’ that makes prescriptive claims on more than one area of scientific research but is not necessarily applicable to all scientific activity.

This analysis is situated in three larger literatures: theories of concepts, conceptual change, and historical epistemology. With respect to concepts, my investigative strategy focuses on the ‘molecularism’ of scientific concepts, a feature potentially overlooked due to reductionist research heuristic biases, but does not support any particular philosophical or psychological theory of concepts. With respect to conceptual change, the heterogeneity of ‘conceptual change’ led us to focus on ‘non-semantic’ issues surrounding incommensurability (differences in methodology or explanatory aims). These are directly relevant to disciplinary syntheses such as Evo-devo in contrast to reference-centered studies in earlier philosophy of science. With respect to historical epistemology, the themes in my analysis show similarities to the historically oriented philosophical research of Canguilhem, Hacking, and Arnold Davidson, which allows for the emergence of cognate ideas such as theoretical and disciplinary polyvalence.

7.5.2. Chapter 2

One of the questions emerging from the claims of Evo-devo proponents is whether innovation and novelty constitutes a distinct problem or research program. The notion of a problem agenda, introduced in Chapter 1 to anchor conceptual clusters, connects with non-semantic incommensurability issues (differences in goals, criteria of explanatory adequacy, methodology, disciplinary interaction) and allows us to address this question apart from a focus on theories or methodology, as is common in much philosophy of science. *Problem* refers to an unknown aspect rather than a knowledge structure or method of investigation, and *agenda* highlights the multifaceted nature of the unit (i.e. many different problems or questions of different kinds). Problem agendas are composed of 'big' questions abstracted from research questions utilized by scientists in ongoing investigation. Many problem agendas exist in biology and they bear particular relations to one another.

Two core issues must be addressed for problem agendas: individuation and characterization. Relying on resources from Aristotle, individuation can be accomplished by paying attention to the relations among problem agendas that derive from particular theoretical constraints and presuppositions. The structure of problem agendas was explicated on analogy with van Fraassen's theory of explanation in terms of answers to why questions, which provided scaffolding for characterizing problem agendas. The problem agenda of evolutionary innovation and novelty can be individuated from that of adaptation on both historical and philosophical grounds. Historically, adaptation was tackled in distinct disciplinary approaches in contrast to innovation and novelty, as well as being extant as a problem agenda prior to innovation and novelty. Philosophically, the tripartite conditions for the operation of natural selection provide the theoretical constraints needed to separate adaptation from innovation and novelty. Using Aristotle's strategy of partitioning different but related questions in terms of appropriate answers, the problem agenda of innovation and novelty was shown to concern the origin of qualitative variation at particular phylogenetic junctures. Instead of phenotypic continuity (gradualism versus saltation), innovation and novelty is about developmental accessibility between ancestral and descendant genotype-phenotype mapping relations. Natural selection is a boundary condition, assumed to be operating but not explanatory. The intrinsic/extrinsic dichotomy does not capture this difference since environmental effects on development in the form of phenotypic plasticity are relevant.

Three basic dimensions characterize the problem agenda of innovation and novelty: form versus function, level of biological hierarchy, and generalization. For form versus function, novelties (form) are terminologically distinguished from innovations (function), and key innovations fall outside of the problem agenda because they foreground the role of natural selection. In contrast to Evo-devo proponents, the distinctness of the problem agenda does not rely on key innovations or different mechanisms underlying variation. For level of biological hierarchy, compositional (part-whole) and procedural (process-organization) hierarchies are distinguished in terms of developmental space (within a generation) and evolutionary time (across generations). A mechanistic explanation of qualitative variation at a particular phylogenetic juncture requires attention to the eight possibilities generated for this dimension. For generalization, model organism use comes to the forefront because of the need to model the variation extant at the appropriate phylogenetic juncture. Molecular level generality across taxa does not translate to generality across taxa *across* hierarchical levels due to the dissociation of lower level processes (e.g. gene expression) from higher-level outcomes (e.g. phenotype). The non-transitivity of molecular level generality is referred to as the 'molecular paradox'. Generality can be evaluated along other lines, for both form and function at different levels of hierarchy, including epigenetic processes or biomechanical principles. Integrating these details into the problem agenda structure makes the criteria of explanatory adequacy clear and identifies key features such as presuppositions, theoretical constraints, and the relevance relation.

Problem agendas are superior to problems as analytic units in philosophy of science for several reasons. In contrast to earlier analyses (Toulmin, Popper, Laudan, Koertge, Hattiangadi, and Nickles), problem agendas are not a single kind of problem but rather a variegated unit capturing the heterogeneity of questions involved in explaining a particular suite of biological phenomena. Problem agendas highlight stability across theoretical alterations rather than rapid problem changes and do not focus on rationality or scientific progress. By making criteria of explanatory adequacy transparent, problem agendas allow for the negotiation of disciplinary interactions but do not represent a measure of the problem solving ability of a research tradition. Related units, such as domains and fields, also suffer in contrast to problem agendas because they do not give accounts of individuation, include methodology and techniques, maintain a focus on theories (knowledge structures), do not capture disciplinary differences, and cannot account for how a disciplinary nexus could be concerned with multiple problem agendas. A problem agenda shares with domains and fields the emphasis on relations between units such as integration and synthesis rather than the traditionally favored relation of reduction. Related to these issues is the difference between values in science and explanatory standards in special sciences. The former focuses on rationality and *all of* science while the latter, where problem agendas apply, are more concretely concerned with explanatory burdens in specific research areas and therefore offer more precision in guiding methodological choices through making explicit the criteria of explanatory adequacy.

7.5.3. Chapter 3

This chapter demonstrated the utility of problem agendas in reconstructing and illuminating an existing domain of research on innovation and novelty. Attention was focused on the origin of avian feathers and flight, which was distinguished from the 'origin of birds' that pertained to the problem agenda of classification. Using the structure and characterization of the problem agenda from Chapter 2, eight questions were evaluated for each avian feature.

- What is the *explanandum* phenomenon? How is the origin of the feature a qualitative departure from an ancestral condition?
- What is the particular phylogenetic juncture under consideration for this feature? What is the disciplinary contribution of systematics?
- What is the contribution of paleontology for understanding the kinds of variation available at the phylogenetic juncture in question?
- How is there a discrepancy between states of variation past and present? What is the contribution of ontogenetic studies to understanding the developmental accessibility between ancestor and descendant genotype-phenotype relations?
- How does the application of the distinctions between form, function, and character bear on analyzing the origin of this feature? What is the disciplinary contribution of morphological investigation?
- How does the recognition of distinct levels of biological organization apply to the origin of this feature? Can we distinguish pertinent compositional and procedural hierarchies, either developmentally (spatially) or evolutionarily (temporally)?
- How does the issue of generality apply to the origin of the feature? How does the molecular paradox apply and what explanatory principles are available or relevant?
- What major research questions are associated with the origin of this feature? What kinds of solutions have been offered?

The origin of feathers (novelty) consisted of explaining the emergence of ancestral feather tracts, which required reconstructing the nature of this phenomenon given existing phenotypic diversity. Feathers are a qualitative departure from reptilian scales and the phylogenetic context for their origin is a theropod-like ancestral taxon. Paleontological contributions come from multiple discoveries of 'feathered' theropods in the past decade. Developmental genetic studies in chickens have uncovered a variety of regulatory and structural genes involved during morphogenesis, although little is known about these features in existing reptilian integuments. Feathers can be joined with multiple functions to generate different characters and this multifunctional capacity indicates the role characters play as theoretical units of integration. A variety of procedural hierarchies in developmental space have been identified but it is less clear how relevant these are to evolutionary time. Considerations of generality indicate that hair and other epithelial appendages are important cross-references, although taxonomic sampling is weak for studies of feathers (chicken) and hair (mouse). The molecular paradox bears on developmental genetic studies that have isolated early acting regulatory genes whose relationship to later ontogenetic events and higher levels of organization are less clear. Research questions and existing partial solutions were then adumbrated.

The origin of flight (innovation) also requires attention to a complex *explanandum* phenomenon because of different flight modes. It is a qualitative departure from the ancestral condition of theropod-like taxa that do not exhibit the feature and paleontological investigation has focused on skeletal elements conducive to certain activities (such as wrist flexing and shoulder rotation), brain size increase, and bone histology. Ontogenetic studies are sparse, at all levels of organization, but wing-assisted incline running results are highly relevant. In contrast to the case of form, multiple form features may underwrite a single function, again drawing attention to the theoretical heterogeneity of character determination. Although there are obvious compositional and procedural hierarchies, their details are not yet understood. The procedural hierarchy in evolutionary time of partitioning the locomotory apparatus into modules is especially relevant for flight origination. Degrees of generalization are purchased via biomechanical principles and behaviors observable in other ‘flying’ animals, both extinct and extant. Taxonomic sampling in this respect is relatively high, although not necessarily representative for the phylogenetic juncture under scrutiny. Many different research questions can be identified and the two main solution strategies are the cursorial and arboreal theories.

Several results emerge from working through these details. First, multiple research questions are at stake and thus the move from problems to problem agendas is extremely appropriate. In addition to multiple questions of different kinds, many different methodologies must be employed. There are significant disparities between the origin of flight and feathers on the issue of function (multiple form features → single function feature) and form (single form feature → multiple function features) and the relevant taxa from which to generalize. These considerations highlight the difficulty of offering complete answers to each research question and, consequently, the difficulty of providing a complete solution to a problem agenda.

7.5.4. Chapter 4

The historical investigation of conceptual use involved in explanations of evolutionary innovation and novelty focuses on the period from 1930-1980. One concern in evaluating whether this topic was ignored, as claimed by some Evo-devo proponents, is the issue of identifying historical sources relevant to Evo-devo. Existing historical studies from historians, philosophers, and biologists tend to use a historiographic principle of choice focusing on the separation of genetics and embryology, with the subsequent exclusion of the latter from the Modern Synthesis. These genetics and embryology exclusion histories primarily concentrate on two disciplines, population genetics and developmental genetics, when considering the reunion of evolution and development in Evo-devo. A primary difficulty confronting these histories is that they capture the ‘lineage of tools’ from experimental embryology that produced the developmental genetics methodology currently used but miss the problems exercising Evo-devo biologists such as the origin of innovations and novelties, which emerge from comparative embryology (a ‘lineage of problems’). Using this distinction between two lineages (problems versus tools), the problem agenda of innovation and novelty can be used as a principle of choice for history relevant for Evo-devo, as long as difficulties of anachronism are recognized. Application of this principle of choice identifies the disciplines of comparative embryology, morphology, and paleontology as the primary homes for studies of evolutionary innovation and novelty during this time period.

A survey of literature on innovation and novelty from 1930 to 1980 shows an abundance of studies from these disciplinary approaches, as well as a scattered variety of others. The difficulty of translating between past and present conceptions is addressed by recognizing that explaining innovation and novelty was primarily referred to as ‘the origin of higher taxa’ during this period, which is indicative of a connection with systematics in these investigations. But this connection was not preeminent as evidenced by the prevalence of functional morphological methodology. In morphological and paleontological research there is a persistent and pervasive appeal to developmental considerations, as well as a bias to the study of novelties (form) over innovations (function). From the perspective of historical studies of innovation and novelty, this was not a ‘quiescent period’ in the history of research juxtaposing evolution and development.

Three exemplars were observed from the traditional disciplinary homes of the problem agenda of innovation and novelty: N.J. Berrill (comparative embryology), D.D. Davis (morphology), and W.K. Gregory (paleontology). Berrill’s comparative embryology of tunicates exhibited mechanical explanations of ontogenetic phenomena, dense taxonomic sampling of species studied, and an interest in the significance of interspecific heterochronies for understanding mechanisms of evolutionary transitions. These features are evident in his explanation of the origin of vertebrates, where he argued that a larger vertebrate-size embryo arose from an ascidian larval form through slippage in the number of cell division cycles relative to the timing of gastrulation. Conceptual themes of his research included morphogenetic fields and self-organization, as well as the centrality of differences in levels of organization in hierarchically constructed organisms, which led him to an anti-reductionist outlook.

Davis, although involved in aspects of the Modern Synthesis, recognized a need for considering evolutionary phenomena at higher levels of organization. To that end he attempted to rectify the lack of appropriate theoretical resources in morphology through the articulation of a new conceptual outlook for comparative anatomical research, much of which was never published. He was intensely interested in evolutionary novelties, observable in his functional morphological study of the shoulder architecture of bears, and the developmental basis for their origination, which helps explain Gould's interest in his panda research. In his panda monograph Davis explicitly considers the morphogenetic mechanisms responsible for differences between pandas and other bears, including the role of epigenetic factors (such as mechanosensitive bone formation), pleiotropy, morphological gradients, heterochrony, and allometry.

Gregory's paleontological research was seen through his massive, eclectic *Evolution Emerging*. There he synthesizes his own research and the work of others with an explicit focus on the origin of novelties. This synthesis of research has the hallmarks of interdisciplinary interaction, recognized by reviews of his book, and was not merely concerned with reconstructing the phylogenetic relationships among taxa. Gregory repeatedly invokes development in explaining the origin of novelties. Although his perspective on ontogeny was broadly Haeckelian, the evolutionary principles he attempted to derive from these various studies show a sophisticated blending of evolution and development.

The significance of studying these three researchers via the problem agenda of innovation and novelty as a principle of choice is apparent in the lack of attention each of them has received from those interested in Evo-devo. Instead of being marked by hostility toward the Modern Synthesis, they are characterized by an interest in the evolution and development of higher levels of organization. This provides a new perspective on the disciplinary inclusion/exclusion dynamics of the Modern Synthesis that emphasizes the style or research perspective involved in disciplinary approaches rather than whether development was left out of or ignored in evolutionary theorizing.

7.5.5. Chapter 5

In this chapter contemporary explanations of innovation and novelty were detailed with special scrutiny on developmental genetics approaches. Developmental genetic tools are currently favored for investigating problems traditionally housed by comparative embryology, morphology, and paleontology. The use of these tools has affected the conceptualization of causation responsible for the origination of features and general principles thought to operate during their origination. A brief survey of *Hox* gene studies in arthropods, as well as other examples (turtle carapace or tetrapod limb), shows the broad contours of these types of explanations. Their structure can be parsed into two, stepwise components: pattern and process. The preliminary aspect of pattern involves the establishment of non-homology and determination of the particular phylogenetic juncture. Gene expression similarities utilized in this aspect have been criticized for not recognizing the dissociation between different levels of organization during the evolution of development and are often executed on widely disparate taxa using regulatory rather than structural genes.

The process aspect involves a mechanistic account of the origin of variation and has primarily concerned spatial and temporal differences (heterotopy and heterochrony) in regulatory gene expression due to *cis* regulatory sequence evolution. These changes can be invoked with respect to an existing gene (co-option) or one or more paralogues (duplication). By definition, these kinds of explanations involve networks of genes, which are often modular in nature or connected with modules at higher levels of organization during ontogeny. Although many other forms of gene regulation exist, they have received less attention in part because they establish a general potential to produce new variation rather than specific regulatory changes leading to new variation at a particular phylogenetic juncture.

These distinctions are applied in two extended case studies. The origin of vertebrate jaws, an old problem from comparative morphology, is set in a phylogenetic context and developmental genetic data from studies of craniofacial ontogeny of chickens, mice, zebrafish, and lamprey species are reviewed. From the various regulatory gene expression identified, contributions to both the pattern and process aspect of explanations of innovation and novelty are identifiable. For pattern, craniofacial relationships of homology between agnathans and gnathostomes are made more complex. For process, key regulatory gene expression patterns include the repression of *Hox* anterior group genes in the mandibular arches and proximal-distal nested expression of *Dlx* paralogues. Neglected but relevant processes were also discussed (pharyngeal arches, dentition, and jaw muscle).

The second case study, ectoderm territories in euechinoids, is complimentary to the first because it demonstrates the operational establishment of non-homology. The direct developing species *Heliocidaris erythrogramma* does not establish oral and aboral ectoderm territories, as is the case for indirect developing species such as *Heliocidaris tuberculata*, but rather has a single extravestibular territory. Molecular and morphological evidence from these closely related species, as well as recognizing heterochronies in developmental sequences, indicates that the extravestibular ectoderm of *H. erythrogramma* is not homologous to either ectoderm territory of *H. tuberculata* and therefore an evolutionary novelty.

Seven different disciplinary approaches were explored to uncover their explanatory strategies regarding evolutionary innovations and novelties. Evolutionary genetics (population and quantitative genetics) expressed a high level of resistance to accepting the presupposition that innovations and novelties are genuine variation phenomena in need of distinct explanation. Quantitative genetics approaches can be sensitive to developmental parameters, although their preferred metric for phenotypes encourages a conceptualization of innovation and novelty in terms of phenotypic continuity rather than developmental accessibility. Comparative development/epigenetics, morphology, and paleontology continue to exhibit many of the features identified in the historical part of our study, especially a focus on higher levels of organization. Comparative development has focused on heterochrony occurring in developmental trajectories whereas epigenetics has called attention to self-organization phenomena, physical properties of cells and tissues and their interactions, and the role of mechanosensitive aspects of ontogeny.

Morphology still represents an abundance of research on innovations and novelties, and consistently invokes developmental processes as causal factors. Researchers in this domain are sensitive to the interconnections among form and function features at higher levels of organization and asymmetries in studying form versus function. Paleontological researchers also continue to rely on developmental considerations and focus on key transitions, such as the origin of the tetrapod limb, but show particular affinities for appealing to the environment extrinsic to organisms. Origination (innovation and novelty) and diversification (key innovation) are not always conceptual separated but the patterns documented for the origin of innovations and novelties at particular phylogenetic junctures constrain the process aspect of explanations.

Behavioral biologists focus almost all of their attention on innovations, in contrast to the bias toward novelties in other approaches, with special attention paid to foraging strategies. The tricky relationship between behavior and evolutionary change lurks in these types of explanations. Although a number of ecological studies of *key* innovation have been executed, the relevant domain from ecology and environment concerns phenotypic plasticity, which concentrates on environmental inputs that affect ontogeny by producing new variation. One prominent argument is that qualitative phenotypes arising from norms of reaction within species explains the origin of qualitative phenotypic differences between species. The environmental factors triggering the expression of these norms of reaction are subsequently taken over by genetic machinery to stabilize the developmental production of the phenotype. Molecular biology and genetics is the 'new kid on the block' in terms of trying to explain the origin of form and function features at the molecular level. Research has addressed the origin of genes, organelles, and biochemical pathways. Very different mechanisms, such as exon shuffling and symbiosis, which involve little to no developmental processes, are invoked as causal factors.

From these different disciplinary approaches, several key themes emerge. There is a pervasive bias toward the study of novelties rather than innovations. Evolutionary genetics is the most antagonistic to countenancing an explanatory burden regarding innovations and novelties. Comparative embryology/epigenetics, morphology, and paleontology exhibit a high degree of continuity when compared with past research, including the conflation of key innovation with innovation or novelty and the origin of higher taxa with the origin of innovations or novelties. Because of the connection with systematics, these three disciplinary approaches keep the specific phylogenetic juncture in view. Developmental genetic explanations sometimes exhibit confusion between the pattern and process components of explanations and lack specific attention to the narrative of change involving multiple molecular level activities. The role of extrinsic factors in ontogeny is largely excluded by virtue of laboratory conditions for culturing embryos. Different disciplinary approaches exhibit affinities for one another. Besides comparative embryology, morphology, and paleontology, there are also connections between functional morphology, ecology/environment, and behavioral biology. Although the extensive use of disciplinary approaches as a unit of analysis much be treated with caution, there is reason to hold that the patterns identified are robust.

7.5.6. Chapter 6

Four domains utilizing the foregoing material make up the analysis in this chapter: interpretations and comparisons, consequences, evaluation, and implications. 'Interpretations and Comparisons' consists of the reconstruction of conceptual clusters for five historical and eleven contemporary explanations from varying disciplinary approaches, and comparison (synchronic and diachronic) of these conceptual clusters. Despite the wide diversity of concepts in use and the suppression of the disciplinary approach of systematics, a number of striking patterns emerge. Both historical and contemporary explanations are biased to explaining entities rather than activities, using activities or relations as their causal concepts, and properties or processes as their evidential concepts. Historical explanations consistently borrow developmental concepts for causes. Contemporary explanations show a dramatic increase in the number of molecular components, which are utilized causally and evidentially to address similar phenomena. The explanatory target concepts representing these innovations and novelties are borrowed in developmental genetics, reflecting the old problems/new tools distinction.

Diachronic comparisons suggest that comparative embryology/development, morphology, and paleontology represent a conceptual cluster equilibrium state but that a reliance on sub-cellular entities and an increase in their overall number appears to have destabilized it. The study of these 'new' entities at their own level of organization in molecular biology and genetics indicates that development is not a significant part of explaining the origin of molecular innovations and novelties. Conceptual change therefore is isolated in the alteration of causal and evidential concepts from higher levels of organization in the conceptual cluster equilibrium state of comparative embryology, morphology, and paleontology through the introduction of multiple new molecular entities. Although the concepts of EVOLUTIONARY INNOVATION and NOVELTY have also added molecular referents, their meaning has not changed. The significant conceptual change involves an increase in the hierarchical gap between the *explanandum* and *explanans*. Conceptual cluster component membership and relations have been altered. Potential ambiguities in or difficulties with these reconstructions are noted in terms of the grain of the conceptual clusters, the choice of characters, the scoring of characters, and taxonomic sampling. None of these prevent a probative analysis of conceptual change in terms of conceptual clusters.

'Consequences' of the analysis of problem agendas were split into individuation and characterization components. For individuation, the distinction between actual sequence and robust process explanations allowed us to see the problem agenda of innovation and novelty as demanding an actual sequence kind of explanation due to the 'at a particular phylogenetic juncture' component. This explanation also necessarily involves developmental biology in order to provide a mechanistic account of the origin of variation, whether from genetic or epigenetic causes. Classification is a related but distinct problem agenda involved in the determination of the phylogenetic juncture. In terms of procedural relations among problem agendas, classification and organismal ontogeny are components of the problem agenda of innovation and novelty, which can in turn be considered a component of the problem agenda of adaptation.

With respect to characterization, each dimension of the problem agenda has various consequences. For form and function, the terminological distinction between INNOVATION (function) and NOVELTY (form) and the conceptual separation of these from KEY INNOVATION is critical. Additionally, the relative neglect of the ontogeny of function, especially at higher levels of organization was observed. For level of biological hierarchy, the tendency to confuse compositional hierarchies in developmental space with those in evolutionary time was flagged, as well its effect on the conceptualization of causality, which is encouraged by the particular developmental genetic tools utilized. Self-organization processes were recognized as a procedural hierarchy and developmental genetic explanations of innovation and novelty exhibit a reductionist research heuristic. For generality, model organism issues concern the closeness of phylogenetic junctures and modeling the ancestral variation capability. The latter, when coupled to the molecular paradox, indicates that a good model system for one level of organization may not be appropriate for another level of organization. Juxtaposing model organisms and the actual sequence explanation demand reinforced the possibility of being unable to causally demonstrate the origin of variation at particular phylogenetic junctures.

The molecular paradox also applies to principles of evolutionary innovation and novelty because processes at one level (such as parcellation at the genic level) may not be appropriate for other levels (such as integration for ectoderm territories). The sociological corollary to the molecular paradox and relative ease of accumulating evidence regarding form features indicates that more data will continue to arrive concerning form at lower levels of organization, potentially skewing explanatory frameworks. Reflecting these consequences into the case study of the origin of vertebrate jaws isolates difficulties with developmental genetic explanations of innovation and novelty more concretely. Developmental genetic approaches generally suffer from an embarrassment of explanatory riches because the cited possible changes in gene regulation offer too much potential for evolutionary change and make it difficult to pin down the actual sequence explanation. Other disciplinary approaches are deficient but in different ways, which indicates the need to appropriately combine them in a complementary fashion.

'Evaluation' took up the claims from Evo-devo proponents regarding the unique potential of their research area to offer explanations of innovation and novelty. Although the exact disciplinary composition of Evo-devo is debatable, biologists agree that disciplinary approaches are not currently meshed. A prescriptive resolution is offered in favor of Evo-devo as a multidisciplinary synthesis, in order to be in a position to have the necessary conceptual resources to address the problem agenda of innovation and novelty. Attention to the criteria of explanatory adequacy indicates that some of the explicit goals of Evo-devo may need to be revised (e.g. explaining form only). How the synthesis of disciplines is to be accomplished to produce integrated explanations is addressed through the ideal of a maximal conceptual cluster. This represents the necessary conceptual resources for form and function at all levels of the biological hierarchy across different taxa within the context of the pattern-process structure of explanations of innovation and novelty, including their locus of contribution and procedural relations. Maximal conceptual clusters are likely to be unstable because of the sociological corollary to the molecular paradox and thus may not be capable of long-term maintenance nor sustain a disciplinary synthesis.

The model of complimentary disciplinary contributions to integrated explanations connects with discussions of explanatory pluralism in philosophy of biology. In addition to the recognition that actual sequence and robust process explanations are not always compatible, differences in problem agendas with distinct contrast classes of answers, complimentary contributions to different aspects of the same explanation (pattern and process), and competition over the relative importance of particular processes within an aspect of the explanation all enlarge and refine the existing discussion of explanatory pluralism. Each of these also bears on interdisciplinary epistemology, with the entire model being characterized as a combination of modest unification and explanatory, concrete integration. It is applicable to other life science disciplinary syntheses, especially those founded on disparities in levels of organization. One key consequence of the difficulty of completely solving problem agendas is that typical grant funding cycles are unlikely to be adequate. Although there is no epistemological need for Evo-devo to be more than multidisciplinary with respect to the problem agenda of innovation and novelty, interdisciplinary activity leading to the formation of a new discipline may be a sociological prerequisite to meet these epistemological demands.

'Implications' focused on the issue of evolutionary theory and its adequacy in dealing with the problem agenda of innovation and novelty. Despite difficulties concerning the nature of evolutionary theory, different interpretations suggest some alteration in order to deal with this problem agenda, either in the modification of assumptions in evolutionary genetics or the recognition of a neglected domain of problems in neo-Darwinism. Ordered sets of problem agendas are suggested as an alternate strategy for characterizing the nature of evolutionary theory. Although the adequacy of natural selection has been impugned historically when researchers were concerned with explaining innovation and novelty, our analysis locates the issue with the *existence* of natural selection as a consequence of the origin of variation at particular phylogenetic junctures. This highlights how different causes are appealed to in evolutionary explanations and therefore the causal power or *adequacy* of natural selection is not in question. Philosophical interpretations of natural selection as merely statistical are thus not required to reconcile evolution and development and, additionally, are deficient in capturing the issues surrounding the problem agenda of evolutionary innovation and novelty.

7.5.7. Chapter 7

In this chapter we covered three basic areas touching on other domains in philosophy of science. The first concerned whether the methodology adopted in this study can be applied to other philosophical investigations of science. The broad procedure of the methodology is readily applicable to other areas of science but the analytic units used, conceptual clusters and problem agendas, may be less applicable outside of biological sciences. Although there is flexibility in using this procedure (choosing different aspects of scientific practice or utilizing different operationalized units), the details of the procedure are recommended because historical investigation, the use of foundational problems and the particular analytical units, as well as drawing prescriptive conclusions, were central to the effectiveness of the study.

The second topic was the testability of philosophical claims about conceptual change. Much of the impetus to study science ‘scientifically’ derives from the desire to import the precision of the testing mechanisms available to scientists, such as modeling scientific change in terms of selection mechanisms. But there is more to empirical evaluation, something observable by attending to the role of interpretation in philosophical exegesis. A broader view of empirical evaluation encompasses statistical testing, problem solving effectiveness, and comparisons with philosophical criteria of adequacy. Conceptual clusters and problem agendas successfully meet previously articulated constraints and desiderata on an account of conceptual change.

The third topic was outstanding questions arising from the dissertation. Some of these pertained to general philosophy, such as whether inferential or conceptual role semantics should be used to add a component of meaning to conceptual clusters, whereas others, such as the applicability of problem agendas to physical science phenomena or the role of conceptual cluster equilibrium states in understanding ‘normal science’, touch on core issues in philosophy of science. Each of these questions, as well as arguments over the analysis and results of this dissertation, are ample fodder for future historical and philosophical studies of science.

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