



Mass extinctions as major transitions

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Abstract

Both paleobiology and investigations of ‘major evolutionary transitions’ are intimately concerned with the macroevolutionary shape of life. It is surprising, then, how little studies of major transitions are informed by paleontological perspectives and. I argue that this disconnect is partially justified because paleobiological investigation is typically ‘phenomena-led’, while investigations of major transitions (at least as commonly understood) are ‘theory-led’. The distinction turns on evidential relevance: in the former case, evidence is relevant in virtue of its relationship to some phenomena or hypotheses concerning those phenomena; in the latter, evidence is relevant in virtue of providing insights into, or tests of, an abstract body of theory. Because paleobiological data is by-and-large irrelevant to the theory which underwrites the traditional conception of major transitions, it is of limited use to that research program. I suggest that although the traditional conception of major transitions is neither ad-hoc or problematically incomplete, its promise of providing unificatory explanations of the transitions is unlikely to be kept. Further, examining paleobiological investigations of mass extinctions and organogenesis, I further argue that (1) whether or not transitions in paleobiology count as ‘major’ turns on how we conceive of major transitions (that is, the notion is sensitive to investigative context); (2) although major transitions potentially have a unified theoretical basis, recent developments suggest that investigations are becoming increasingly phenomena-led; (3) adopting phenomena-led investigations maximizes the evidence available to paleobiologists.

Keywords Major transitions · Paleobiology · Mass extinctions · Organogenesis

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Introduction

A body of work in evolutionary biology understands life's history by positing crucial, 'game-changing' events—*major transitions*—which explain patterns in the diversity, complexity and disparity of life. Paleobiologists also care deeply about the events and processes which shape life's trajectory on the macro-scale, and posit events—*mass extinctions* for instance—which play similarly game-changing roles. These discussions are oddly disjoint: in particular, evolutionary theorists concerned with major transitions don't attend in detail to paleobiological evidence or paleobiological theorizing. If their subject-matter or interests overlap this is surprising.

There are many reasons why research programmes might fail to be in dialogue. Institutional differences often play a role. The major transitions literature is firmly rooted in evolutionary biology, while mass extinctions are studied by paleobiologists, and flow between these disciplines (particularly from the latter to the former) is rare. Further, although both projects are interested in 'the shape of life' their actual explanatory targets often differ. Where the paleobiologist is interested in patterns as revealed by the fossil record, evolutionary biologists often investigate patterns in living biota. Such factors surely play their part in explaining the lack of flow from paleobiology into the major transitions literature. I'm going to argue that this disconnect is revelatory of a difference in how paleobiologists on the one hand, and some evolutionary theorists on the other, approach questions about macroevolution. As we'll see, evolutionary theorists attempt to provide a *theory-led* explanation of life's shape. Abstract details of the basic mechanics of evolution are front and explanatorily centre. This leads to a particular methodological strategy: explaining how minimally specified systems might evolve the properties associated with major transitions. By contrast, paleobiological investigations are often *phenomena-led*. They are primarily concerned with actual patterns in the fossil record, and how these are revelatory of the biological, geological and environmental processes which generate such patterns. As such, their methodological strategy is more diverse, bringing to bear a wide range of evidential sources. So, this paper is not only about the lack of discussion between paleobiology and neontology. Examining the differences between how paleobiologists approach macroevolution and how evolutionary theorists approach major transitions reveals two different ways of investigating life at the broadest of scales.

In addition to shedding light on the relationship between paleobiology and neontological investigation of major transitions, I'll suggest that the phenomenaled nature of paleobiology brings insights concerning paleobiological success. There is an occasional pessimistic streak regarding the epistemic power of paleobiology (and the historical sciences more generally): given that experiments are of limited relevance, and that the deep past's signal is often biased, degraded and incomplete, we shouldn't expect paleobiology to be as successful as, say, 'experimental' sciences (see, especially, Turner 2007). More optimistic conceptions emphasize the 'disunified' and 'opportunistic' method historical scientists adopt, especially Wylie (1999, 2002; Chapman and Wylie 2016) and myself (Currie

2016, 2018). I'll argue that the phenomena-led character of paleobiology helps explain the nature of this disunified strategy and why it is adopted.

I'll begin with first passes at both major transitions and mass extinctions, before characterizing 'phenomena-led' and 'theory-led' investigations. I'll then revisit major transitions and argue for a context-sensitive conception. That will underwrite a discussion of how transitions are treated in paleobiology (illustrated by both mass extinctions and the evolution of vertebrate limbs). I'll finish with a discussion of how conducting phenomena-led investigations contributes to the success of historical reconstruction. In the conclusion, I'll make a few comments about the relationship between paleobiology and neontology.

Major transitions

Life might unfold gradually, or it could be shaped by game-changing events. Maynard-Smith and Szathmáry (1997) called such events *major transitions*, and identified two types. First, shifts in the mechanisms of inheritance (that is, in information-transmission); second, the emergence of new levels of individuality. The invention of sex enabled genetic recombination via meiosis; multi-cellularity enabled significantly increased mechanistic specialization. Events like these are important not simply because of the magnitude of the changes they wrought, but because of the nature of those changes: they alter the space of evolutionary possibility itself. As Calcott and Sterelny put it:

Instead of conceptualizing life as evolving through a fixed, though immense, space of organic design, and asking how that space is explored over time, Maynard-Smith and Szathmáry conceived of the space of biological possibility as itself evolving (Calcott and Sterelny 2011, p. 4).

A major transition, then, involves a shift in biological possibility. For instance, there are basic limitations on how large a single-celled organism can be. By banding single cells together, multi-cellular organisms can achieve much greater sizes. In transitioning from a single-celled mode to a multi-cellular mode, then, different areas of possibility space become occupiable.

Why do Maynard-Smith and Szathmáry focus on the events they do? They are aware that there are other important events in life's history:

[We] have not included major phenotypic changes, such as the conquest of land by plants and animals, or the origin of vision, or of flight or of homeothermy, which did not involve such a change in the method of information transmission (1997, p. 6).

What is so important about information transmission and the emergence of new evolutionary individuals? On Calcott and Sterelny's reading (2011), what makes a major transition *major* is that it involves modifying "...core elements of the evolutionary process itself" (4). It is thought that there are minimal conditions for a population to be subject to evolutionary forces (Lewontin 1970; Godfrey-Smith 2009).

Say, for adaptations to accumulate there must be sufficiently high-fidelity transmission of traits across generations. A major transition has profound effects in virtue of modifying these core elements. Heredity via cloning generates a different set of dynamics than heredity via sex, and this explains why life's shape differs for cloning and sexual populations.

This underwrites a view of life's shape that is both *punctuated* and *contingent*. 'Punctuated' because between major transitions, life obeys a set of rules governed by some basic dynamics; life's shape radically alters only when those dynamics shift. An old business-as-usual is replaced with a new business-as-usual. 'Contingent' because there is often nothing inevitable about the occurrence of major transitions—the right conditions must hold, and these are not guaranteed, and moreover the mechanisms which underwrite and generate the core evolutionary dynamics are themselves multiply realizable ("Different mechanisms may be involved in the origin and the maintenance of higher-level organization" Maynard-Smith and Szathmary, p. 9).

Maynard-Smith and Szathmary made explicit an explanatory regime based on the unity they see in the major transitions they identify: the emergence of new units of selection.

Why did natural selection, acting on entities at the lower level (replicating molecules, free-living prokaryotes, asexual protists, single cells, individual organisms), disrupt integration at the higher level (chromosomes, eukaryotic cells, sexual species, multicellular organisms, societies)? It is because there is this common question that we have found it illuminating to compare the different transitions (Maynard-Smith and Szathmary 1997, p. 7).

And the kind of question Maynard-Smith and Szathmary propose is amenable to analysis via the abstract explanatory machinery of population genetics, game theory, and the like. We explain how the inherent selfishness of individuals are overcome in order for a common fate to emerge. Sharing a common fate makes cooperation of various stripes fitness-enhancing, and thus so too mechanisms which dampen cheaters. Under the right conditions, these can underwrite the emergence of a new evolutionary individual, itself consisting of previously competing parts.

Maynard-Smith and Szathmary's work has provided much fodder for philosophers and theoretically-inclined scientists. Common questions concern the unity or otherwise of major transitions (McShea and Simpson 2011; O'Malley and Powell 2016), characterizing the kind of explanations involved (Calcott and Sterelny 2011), and so on. These discussions will matter later, but for now let's consider what evidence might be relevant to understanding major transitions.

At the opening of *The Major Transitions of Evolution*, Maynard-Smith and Szathmary discuss a crucial epistemic question: how might we test claims about major transitions? The evidential sources they don't mention are telling.

There are obvious difficulties in discussing unique events that happened a long time ago ... [however] we have agreed theories both of chemistry and of the mechanism of evolutionary change. We can therefore insist that our explanations be plausible both chemically, and in terms of natural selection. This

places a severe constraint on possible theories... Further, theories are often testable by looking at existing organisms (Maynard-Smith and Szathmary 1997, p. 3).

Maynard-Smith and Szathmary appeal to theoretical constraints and neontological evidence in defending the epistemic tractability of their explanatory program. The experimental approach involves using animal models to simulate transitions under artificial conditions (c.f., Godfrey-Smith 2006). Theoretical modelling results both inform us about possibility under constraints and are used to generate explanations of how major transitions occur. Paleontological evidence is a glaring omission. First, paleobiologists, as we'll see below, are clearly concerned with understanding life's shape at the macro-level. Second, presumably fossils and other paleobiological evidential fodder are relevant to 'unique events that happened a long time ago'. Third, today's living biota are but a tiny speck in the ocean of deep time: their representativeness, their capacity to tell us much about the past without supplementation or integration with fossil data, can be questioned (Marshall 2017). This motivates a switch in topic: let's consider how paleobiologists go about understanding life's shape.

Mass extinctions

Like Maynard-Smith and Szathmary, paleobiologists often see life as shaped by game-changing events. However, they pick out quite different transitions. Here, I'll focus on one class of these: mass extinctions (later on we'll meet another set concerning the evolution of vertebrate limbs).

Just as death is part of an individual's life, so too is extinction part of the life of a species. In individual populations there are continual deaths (and births); in the fossil record there is a 'background' rate of extinction-events (and speciation events). However, there are spikes against these backgrounds. An enormous spike in the rate of human death occurred at the beginning of the Colombian exchange in the sixteenth Century (Crosby 2003); for dinosaur-species, an extinction-spike occurred around 66 million years ago. These spikes—mass extinctions—have mattered to paleobiologists at least since the early 1980s. Studies of mass extinctions concern (1) empirically characterizing the patterns in the fossil record, (2) determining the biological or geological nature of the signals, (3) considering processes or mechanisms which could generate those patterns, (4) considering the implications of such events for life's shape (see Currie 2018 chapter 7, section 7.1.2).

Fischer and Arthur (1977) and Raup and Sepkoski (1982) used statistical analyses of the appearance and disappearance of marine fossils to challenge the view that extinction should be modelled as a gradual, continual process. They thus characterized a pattern in the fossil record (one assumed, with good reason, to be biological). Raup and Sepkoski in particular claimed to have uncovered 12 spikes and suggested that these occurred periodically on a 26 million-year cycle. With the pattern in place, processes or mechanisms were then hypothesized. Raup and Sepkoski contrast biotic causes with "... recurrent events or cycles in the physical environment"

(805), suggesting that extra-terrestrial events could explain the periodicity.¹ In light of such mechanisms, they drew macroevolutionary considerations:

The implications of periodicity for evolutionary biology are profound. The most obvious is that the evolutionary system is not “alone” in the sense that it is partially dependent upon external influences more profoundly than the local and regional environmental changes normally considered (805).

That is, the biology-focused machinery of evolutionary theory is insufficient to explain life on the macro-scale, due to non-biological sources of contingency (McConwell and Currie 2017). Further, mass extinctions make a difference:

With kill rates of species estimated to have been as high as 77% and 96% for the largest extinctions, the biosphere is forced through narrow bottlenecks and the recovery from these events is usually accompanied by fundamental changes in biotic composition. Without these perturbations, the general course of macroevolution could have been very different (805).

In Raup and Sepkoski’s foundational paper, then, the four features listed above are more-or-less present. Since then, investigations of mass extinctions have become increasingly sophisticated and diverse. One development has been the use of simulations to theoretically probe the features of evolving lineages, including mass extinctions. As opposed to what we see in major transitions, such simulations are typically examined in combination with the fossil record. Another is the inclusion of increasing detail concerning the multitude of causes underwriting extinction spikes. By Erwin et al. (2002), recognized that “... A full understanding of mass extinctions requires an integration of the details of the fossil record, changes in the chemistry of oceans and atmospheres, the tempo of extinction, and the distinction between triggers and mechanisms” (363).

Mass extinctions, then, share features with major transitions. Most profoundly, they change the game: dramatic environmental shifts coupled with extreme biotic turnover affect which parts of possibility space may be occupied by the survivors’ descendants. However, examinations of mass extinctions draw on quite different evidential sources than studies of major transitions. Further, traditionally mass extinctions are not considered major transitions. And, as stated in the introduction, paleobiological discussion of transitions does not appear to be in dialogue with the research program Maynard-Smith and Szathmary began. What gives?

Theory versus phenomena led science

Two central questions emerge from the discussion thus far. First, are mass extinctions major transitions? Second, what explains the absence of paleobiological evidence in the major transitions literature? The former question has, in a sense,

¹ Note that it is no longer thought plausible that extra-terrestrial impacts commonly cause mass extinctions. That appears to be particular to the K–Pg extinction (Schulte et al. 2010).

an easy answer. To be a major vis-à-vis our discussion thus far, an event must constitutively alter the ‘core’ components of evolution. Although mass extinctions may facilitate such changes, they do not do so necessarily as, for instance, the emergence of new evolutionary individuals might. But why accept this definition? If Raup and Sepkoski are right, mass extinctions play a crucial role in the story of life’s shape: they’re major, even if they’re not major transitions. An answer to the latter question will illuminate the former. I’ll suggest that, once we understand what the major transitions literature is trying to do—its goal—we see that paleontological evidence is more-or-less irrelevant. In later sections, I’ll question whether major transitions as traditionally conceived succeeds in meeting aspects of that goal.

Let’s distinguish between *theory-led* and *phenomena-led* investigations. Intuitively, the difference turns on whether the investigators are primarily interested in understanding general theories, or are interested in particular or recurrent events. On the major transitions approach, the main evidential and explanatory work is undertaken by evolutionary theory. At base, a minimal model of evolutionary populations is used, and alterations to that model provide explanations of macroevolutionary change (Calcott 2011). Further, the problems themselves are characterized in terms of those theoretical models: asking questions such as how populations of replicators might overcome competition in becoming a new evolutionary individual.

The theory-led nature of major transition investigation is evident throughout Calcott and Sterelny’s recent collected volume on the topic:

This emphasis [on evolutionary individuality] is reflected in the content of the current volume: The majority of the papers are concerned with some aspect of transitions in individuality. As we have suggested, there is a more expansive way to interpret these transitions—one that involves not just transitions in individuality, but any shift in the core components of the evolutionary process (8).

We have, then, a model of evolutionary processes. It consists of some core components—notions of ‘fitness’ or ‘replicability’, for instance. A major transition is a shift in those core components. It is presumed that major transitions occurred, but precisely when, over what period of time, or via what actual mechanism or process, is largely irrelevant. What matters is understanding how a set of general problems pertaining to the possible occurrence of transitions between different evolutionary dynamics are overcome.

Study of mass-extinctions is, by contrast, *phenomena-led*. The central concerns involve characterizing, finding evidence of, and explaining both particular events in the fossil record, and patterns across it. As such, timing, scale and actual mechanisms or processes are crucial to the questions being asked. As we saw, Raup and Sepkoski undertook a data-intensive, statistical analysis of the marine fossil record. This involved gathering data, generating phylogenetic hypotheses, and then identifying spikes against background extinction rates. With this in place, hypotheses are posited about the causes of the mass extinctions and are tested using an array of empirical strategies.

The distinction between phenomena-led and theory-led can be made precise by appeal to evidential relevance.² Brigandt (2010) and Love (2006) argue that the explanatory or evidential role some information may play in an investigation depends on context, specifically the ‘problem agenda’ at hand. Problem agendas set criteria for explanatory adequacy, which govern the roles different evidence or data might play. Here’s Love on problem agendas:

[a problem agenda] is a “list” of interrelated questions (both empirical and conceptual) that are united by some connection to natural phenomena. For example, how do questions concerning greenhouse gas contributions from plant respiration, along with many other questions about emission-related phenomena (anthropogenic or otherwise), including their interaction with systematic cycling and atmospheric dynamics, get answered with respect to global warming phenomena? (877).

Such problem agendas are structured by ‘general criteria of explanatory adequacy’ which set which kinds of questions should be answered (and how) within that agenda. Brigandt takes some lines of evidence to form the ‘core’ of a research agenda: they provision the explanation of the phenomena in question, while other lines of evidence play supporting roles. How this operates is best demonstrated via exemplar, so let’s turn again to our problem agendas: mass extinctions and major transitions as described in the previous two sections.

Major transitions, as described thus far, is a problem agenda built around questions concerning the ‘rules’ of evolution: that is, how evolutionary individuals, populations and the mechanisms of heritability change over time. Questions include: how could a population of competing conspecifics overcome the temptation to defect? How do changes in pathways of heredity change evolutionary dynamics? Notice that the ‘phenomenon’ in this circumstance is *theoretical*: it concerns the dynamics of evolutionary populations.

What about the general criteria of explanatory adequacy in this domain? As we saw, Maynard-Smith and Szathmari point to the constraints of chemical and evolutionary theory on hypotheses of transitions, and use evolutionary theory to articulate their questions and their answers about heredity and individuality. The model-based explanations provisioned by evolutionary theory, then, form the ‘core’. Modeling is relevant because it reveals the nature of said theory; some neontological lab-based studies are relevant because they provide insight into the capacities of systems meeting those minimal requirements. In contrast, the long-range, deep-historical information about particular times and places, and patterns across times and places, affording by paleontology seems largely irrelevant. After all, such information neither constrains nor provides

² The distinction between *phenomena-led* and *theory-led* investigations has close kin in Weisberg’s (Weisberg 2007) distinction between ‘model-based’ and ‘abstract-direct representation’ (ADR) strategies in science. Like model-based strategies, theory-led investigations often involved conceiving of some phenomena abstractly, and investigating that phenomena using theoretical models. And like ADR, phenomena-led investigations often proceed by building an empirical picture of a phenomena via data collation. However, how we articulate these distinction is quite different, and phenomena-led investigations are a much broader category than Weisberg’s ADR.

insights into the behaviors of the minimal evolutionary systems with which the theory-driven investigations of major transitions concern themselves.

The problem agenda of mass extinctions includes questions about the periodicity or otherwise of spikes in extinction rates, to what extent the signal is geological or biological, what kinds of events enable or trigger mass extinctions, and questions about the downstream effects mass extinctions could have on the shape of life. General adequacy is here indexed to the pattern at hand (as opposed to some theory): data-gathering techniques and data-analysis matter, as do hypotheses about the fates of particular lineages, general trajectories, and the biotic and abiotic causes of extinctions. As such, the modeling and neontological studies favored by the major transitions folk are often valuable (particularly in hypothesizing about potential mechanisms or processes), but so also is long-range fossil and paleoclimatological evidence.

So, we can distinguish between *phenomena-led* investigations, where the problem agenda appeals to some ‘phenomena’, that is, a possibly re-occurring occurrence that is observed or measured; and *theory-led* investigations, where the problem agenda appeals to a specific body of theory. It is important to note that this distinction is *not* the same as that traditionally drawn between ‘experimental’ and ‘theoretical’ science, nor between ‘natural history (idiographic)’ and ‘nomothetic science’, nor between ‘hypothesis-driven’ and ‘data-driven’ science. Phenomena-led investigations are rich in hypotheses, make use of theory (perhaps even laws!), and do not necessarily require extensive data-gathering prior to forming hypotheses; theory-led investigations are not necessarily impractical, divorced from the world, or speculative. The difference turns on whether it is phenomena or theory which set the problem agenda—provisions the explanatory core—and thus sets the criteria for adequacy. Continuing from this, the distinction doesn’t turn on the intentions of scientists, but the structure of their investigations. Further, the distinction is not necessarily discrete nor complete: although some investigations may be more ‘purely’ phenomena- or theory-led, it is not part of my view that any particular investigation can be slotted neatly into either category. Note also that investigations may be dynamic regarding their being theory-led or phenomena-led: one may shift between the two. I’ll provide some reason to think this is happening for major transitions below.

With this distinction on the table, we can restate a preliminary result: By my analysis, paleontological evidence is not included in discussion of major transitions for good reason. For theory-led investigations, evidence is relevant when it provides constraints on both how a minimal system ought to be specified, and on the capacities of such systems. For phenomena-led investigations, evidential relevance is due to explanatory features of the phenomena at hand. The theory-led nature of the major transitions literature renders much paleontological evidence irrelevant.

Narrow and broad conceptions of major transitions

Since Maynard-Smith and Szathmary’s original publication, conceptual discussion of major transitions centred on a tension between the desire for a unified or theoretically grounded notion and a desire for completeness—that is, to capture the events

which in fact shaped life. In this section, I offer a way of understanding these differences, and critically examine various responses to that tension.

Distinguish between *sources* and *outcomes*. The ‘source’ of a transition is the kind of event which underwrites it: the emergence of a new individual, say. The ‘outcome’ of a transition is the macro-evolutionary pattern which emerges in light of that event: the radiation of a lineage, say (the distinction between ‘source’ and ‘outcome’ is from McConwell and Currie 2017). Conceptions of major transitions can be restricted via the admissible sources or admissible outcomes. In their original formulation, Maynard-Smith and Szathmary provided a fairly narrow account. Only macro-evolutionary events caused by the emergence of new individuals, or new means of transmission, counted. Samir Okasha and some others (Okasha 2005; Michod 2007) restrict transitions even further: to the emergence of new individuals alone. Specifying a relatively small set of sources enables the accounts’ theoretical unity, and thus its capacity to be theory-led. There is a cost however: many events which certainly mattered deeply for life’s history do not count as major transitions, and for some the unity achieved isn’t sufficient. Szathmary himself develops a broader account (2015) while attempting to retain theoretical unity, while O’Malley and Powell (2016) adopt a yet more permissive account which includes differences in metabolic processes. On my view, the way into major transitions implied by Calcott and Sterelny above does suggest a theoretically-unified, relatively narrow way of conceiving of major transitions. Most discussions focus on sources but, as we’ll see, I suspect a tacit restriction on outcomes operates in the traditional view. I’ll first respond to a set of objections which claim that the traditional approach to major transitions is either incomplete or ad-hoc, before turning to what I think is a more pressing objection.

Ad hoc and incomplete?

Commentators complain about the apparent ‘hodge-podge’ of events identified in the original major transitions (McShea and Simpson 2011; Ågren 2014; O’Malley and Powell 2016)—the objection being that the inclusion or exclusion of events is ad-hoc. Surely a list including such disparate events as the emergence of cultural societies and multi-cellular organisms is disunified, after all, the inclusion of these quite different events requires different justifications. This is too quick. If major transitions are supposed to be game-changing vis-à-vis evolutionary theory, then an event’s inclusion turns on it altering core evolutionary mechanics. For Maynard-Smith and Szathmary’s original view, those mechanics were conceived of in a fairly traditional way: a population undergoes evolution just when individuals in that population (1) have traits of differing fitness which (2) are heritable. The emergence of new individuals opens the door to new traits, and new pathways of heredity (or information-transmission more generally) can alter evolutionary dynamics. Insofar as those criteria are unified via that conception of evolutionary processes, they are no hodge-podge. So, the charge of ad-hocness strikes me as under-motivated.

O’Malley and Powell stress two senses in which ‘major transitions’ are incomplete:

- (1) Missing events that do not fit the... criterion, but which are so transformative from a macroevolutionary perspective that they must be included, and
- (2) missing events that fit the... criterion, but which nonetheless have been excluded... (166).

In other words, first, some events are not game-changers vis-à-vis the rules of evolution, but surely are game-changers vis-à-vis life's history. O'Malley and Powell emphasize the great oxygenation event: the evolution of photosynthesis transformed global climates from anaerobic-favoring to aerobic-favoring. "Oxygenic photosynthesis is a biological innovation that altered in a sustained way the selective regimes and evolutionary trajectories of the main branches of the tree of life" (168). This enormous metabolic change likely enabled the evolution of new kinds of individuals and new means of heredity, but did not in itself count as such, so, it is not included in narrow conceptions of major transitions.

And, second, other events do count as a change in evolutionary dynamics, yet are excluded from being major transitions. O'Malley and Powell point to plastid acquisition: the fusion of a photosynthesizing cyanobacteria with a eukaryotic cell which enabled the evolution of blue-green algae and plants. This is surely the emergence of a new kind of individual, and one with dramatic macro-evolutionary consequences, especially in light of the role of plants and blue-green algae in global oxygen cycles. Yet it was excluded from early discussions (although Szathmáry for one has since changed his mind on this). More generally speaking, given that the emergence of individuals typically involves overcoming cooperative challenges, and these involve the coupling of evolutionary fates amongst individuals, it is tempting to take many events (the forming of social groups, horizontal gene transfer, etc....) as counting as the emergence of new individuals: but many of these stretch the notion of 'major' (from a macro-evolutionary perspective) to breaking point.

On my view, both of these worries are over-overstated. Regarding the former, distinguish between the complaint that the major transitions as originally conceived are unmotivated and arbitrary—a 'hodge-podge'—and the complaint that there are mistakes in which particular events are included or excluded from the list. Even if the exclusion of plastid acquisition was in error, it doesn't follow from this that the more-or-less narrow conception of major transitions, focusing on individuals and heredity, is unprincipled. The list just needs to be corrected. As we'll see, this is Szathmáry's recent aim. Moreover, the worry that there is no way to exclude events that involve new individuals, yet are microevolutionarily minor, ignore what I think is a tacit commitment in the original formulation of major transitions: one which focuses on *outcomes*. Sources are restricted to new forms of heredity and new individuals, and outcomes are restricted to major changes in macroevolutionary patterns. As I'll discuss below, what counts as 'major' is an open question, but I see no reason for this to undermine the research program.

I do think, then, that the two original dimensions (the emergence of new individuals and intergenerational pathways), if coupled with a restriction on outcomes, and when linked to a traditional conception of evolutionary theory, provides a kind of theoretically-unified research program. And indeed, I think this view is clearly present in Szathmáry's (2015) reconceptualization of the major transitions. As he says,

Far from being an arbitrary collection of merely interesting anecdotes about evolution, transition theory has been presented as exploring the topic in two dimensions...this view is linked to the notion of unities of evolution that multiply, show inheritance, and have variability. Uniting the last two criteria in hereditary variability, one has two major features: the nature of multiplication and the nature of inheritance, and we investigate the major evolutionary transitions of these features (10105).

However, even if a theoretically-unified research program is available, it doesn't follow from this that this program is satisfactory. O'Malley and Powell point to biotic events which don't fit within the framework and yet surely count as major events in the history of life. And although mass extinctions are perhaps not as dramatic as the Earth's oxygenation, it is hard to ignore the end-Permian extinction's culling of 96% of all marine species. Based on similar considerations as hold for the atmosphere's oxygenation, ignoring these major biotic events in the service of theoretical unity looks perverse. But this complaint too is, I think, far too quick: Maynard-Smith and Szathmari never claimed that their conception of major transitions is intended to cover all of the game-changing events; just an interesting, theoretically unified sub-set of them. As we saw in the introduction, they explicitly do not claim exclusivity (similar might be said of the charge that the major transitions literature re-creates a 'great chain of being', marching to the human zenith of evolution. So long as the view is not taken to be exclusionary, much of this objection's teeth are removed, at least in principle: it could be that in practice such conceptions encourage problematic thinking).³

On this kind of view, 'major transitions' is a term of art which picks out a particular, interesting, and theoretically unified set of events in life's history.

Pay-offs

Although I think the objections considered above are unfounded, I do think there is a more pressing worry regarding whether the major transitions approach is, or even can, fulfil what it hopes to. To see why, distinguish between two kinds of benefits we might gain from the major transitions literature.⁴ One set concerns *theoretical pay-offs*: investigation of relatively narrow conceptions of major transitions will increase our understanding of evolutionary theory. Another set concerns *explanatory pay-offs*: the idea that we will explain the actual shape of life using the theoretical machinery of major transitions. I think it the theoretical pay-offs have been bountiful, but I have doubts concerning explanatory pay-offs. As we'll see, explanations targeting the traditional major transitions do not turn on the machinery of

³ I suspect that O'Malley and Powell's objection is better put not as being about the arbitrariness or ad-hocness of the major transitions literature, but against the conception of evolutionary theory which underwrites it. If the traditional idea of an evolution as fundamentally involving heritable, fitness-enhancing traits changing populations over generations is a mistake, then perhaps so too are research programs led by that theory. I am far too much of a pluralist at heart to take a stand on that question.

⁴ I'm grateful to Rune Nyrup for suggesting this way of putting the point.

that theory-driven investigation. In fact, we see signs of switching from a theory-led investigation to a phenomena-led investigation. If how we explain major transitions as narrowly conceived doesn't have the payoff it is supposed to, then the framework becomes, it strikes me, considerably less interesting, even by its proponent's own lights.

The benefit of the original framework wasn't simply supposed to be identifying a theoretically unified set of questions, or an opportunity to probe and understand evolutionary theory, but to provision a set of common explanatory resources applicable to actual history. And indeed if a clean explanatory schema could be applied across the major transitions, I would be more amenable to excluding things like mass extinctions from the list. Calcott and Sterelny (2011) has argued for explanatory ecumenism concerning major transitions: that the high-level theoretical explanations of the narrow conception are not in conflict with more complex specific explanations of particular transitions. Although his view relies on what I take to be a typical feature of biological explanation, that "even when we identify a particular biological phenomenon, we can still go about explaining it in a number of ways" (35, 36), I have doubts in this particular instance. It looks to me as if those common explanatory resources are giving way to a series of much more detailed, complex explanations. That is, the simple, broad theoretical explanations in fact fail to explain actual transitions. A closer look at Szathmáry's reboot will suffice to suggest this.

To back up these claims, I'll turn to Szathmáry's reexamination of major transitions (2015). His picture still takes the transitions to be theoretically unified (or at least principled): in the face of increasing complexity over evolutionary time, we posit two kinds of events which involve shifts in 'the rules' of evolution. These can be explained by appeal to a set of common explanatory resources provided by the relatively simple models and equations of evolutionary game theory and the like.

The question can justifiably be raised whether we have a theory or not. I think we do, but with qualifications. Theories do not have to be predictive but still can have considerable explanatory power... if we see, even in rudimentary form, that originally independent reproducing units join, somehow use functional synergies among the units, and that there is some novelty in the inheritance system as well, then the population is definitely on its way to a "major transition" (10110).

This gives the appearance that explanations of major transitions are what I have called 'simple narratives': explanations of particular events which operate by positing a simple model and then demonstrating that the case in hand meets the conditions of that model (Currie 2014; Calcott and Sterelny 2011 calls these 'broad explanatory generalizations'). In such cases, the same explanatory model is often applied across a range of phenomena (perhaps ala Kitcher 1981). However, in Szathmáry's sketch and update of major transitions, this apparent simplicity breaks down. First, he embraces Queller's (1997) distinction between egalitarian and fraternal transitions (the former involves two different kinds of units combining, the latter units of the same type); each require different evolutionary mechanisms to ensure cooperation. Second, the details of how the transitions in fact occurred become increasingly crucial for the explanation, and so the theoretical model starts to fall

from the explanatory picture. Take two examples: the origin of the eukaryotic cell and the emergence of human social groups.

According to Szathmáry, the evolution of eukaryotes is a major transition: the energetic advantages endowed by mitochondria allowed a larger number of genes and lower death rates, and thus more space for evolutionary experimentation. Thus, the space of evolution morphed (however, see Booth and Doolittle 2015). Moreover, it occurred via egalitarian combination. However, the nature of the transition is hotly contested, and turns crucially on matters of phylogenetic order: whether phagocytosis and other distinctive eukaryotic features emerged prior to the acquisition of mitochondria or vice versa. The details are not my concern here, but note that the answer to this question—necessary for explaining the major transition—turns not on game theoretic machinery, but on energy demands. “The major argument against the phagocytosis-early scenario is once again energetic. According to this view, the boost provided by mitochondria not only was necessary for the evolution of very complex eukaryotic genomes, but also was essential for the origin of the eukaryotic condition” (Szathmáry 2015, p. 10107). In other words, the energy-boost provisioned by mitochondria looks like a precondition for the emergence of the other fancy features associated with eukaryotes. The explanatory machinery applied to the transition turns on the energetic demands of the relevant system: it goes far beyond the simplicity implied by the theoretical unity of major transitions.

Take another example: Szathmáry’s discussion of the evolution of the suite of traits associated with the hyper-cooperative social groups distinctive of hominids. Here, he emphasizes the role of increased cooperation leading to the evolution of language (“with its unlimited hereditary potential” 10109), the role of grandmothers as carriers of both genetic and cultural information, and group selection as a means of further decoupling cooperation from genetic relatedness. As he says,

We see key elements that are high-lighted in other transitions: cooperation (including reproductive leveling and food sharing), a form of sociality, a powerful novel inheritance system, and living in groups... It sounds just right: biology gives room to technological and communal cultural evolution. Due to social care (including medicine) and agriculture, the biology of humans has become gradually de-Darwinized. It is culture where the main action is going on (10110).

To my mind, this explanation diverges far from positing the emergence of a new hereditary mechanism or evolutionary individual in light of quashing evolutionary pressures against cooperation. Instead, a complex battery of both particular details about hominid evolution (the evolution of grandmothers, the particular timing of language evolving) are interwoven with the models of evolutionary theory to generate a complex narrative. Theory plays important roles, but it does not *lead*: relevance is set by the event itself, be it hominid evolution or the emergence of eukaryotes. The main action lies in the phenomena.

Recall that evidential relevance makes the difference between phenomena-led and theory-led investigation: in distinguishing the two, we ask whether relevance turns on relationship to theory, or to phenomena. In Szathmáry’s discussion relevance does not turn on testing theoretical machinery, or applying that machinery

to particular cases. If it did, then the energy demands of phagocytosis or the role of grandmothers in hominid social groups would be irrelevant. Rather, relevance is set by the particular phenomena targeted: the evolution of hominid-style cooperation, or the emergence of the prokaryotic cell. Simple, model-based narratives give way to complex, detailed narratives.⁵ There is no problem with this in and of itself (I would be tempted to call it an improvement) but it does undermine Szathmáry's claims to theoretical unity. The course of investigation bucks attempts to maintain the theoretical and explanatory advantages which supposedly justify retaining a narrow conception of major transitions. The explanatory pay-offs of major transitions as narrowly conceived, then, have been overstated.

Are mass extinctions major transitions?

Hopefully you won't be too disappointed that the answer to whether mass extinctions are major transitions is: it depends. Let's summarize the arguments of this section thus far. There are theoretically principled ways of delineating major transitions by restricting both sources and outcomes. Any theoretically unified way of carving up the space is likely to exclude biotic events which made a crucial macroevolutionary difference; this shouldn't be surprising, as being exhaustive was never part of the major transitions project. However, if Szathmáry's (2015) development is representative, then claims to theoretical and explanatory unity are undermined as the details of particular cases swamp the apparent simplicity of the abstract explanatory schemas which motivated the project in the first place.

It strikes me that a natural response is to accept that what counts as a major transition is to at least some extent context sensitive.⁶ In particular, answering whether some phenomenon is a major transition requires specifying a set of sources and a set of outcomes. Coarsely, do we mean major transitions in a narrow, or a broad, sense? The accounts of major transitions that I have surveyed discount major extinctions and yet, if we are sufficiently permissive on the outcome side, it is plausible that the occurrence of mass extinctions, in virtue of their influence on life's shape, can be viewed as major transitions. However, as discussed above, they are not likely to be theoretically unified: investigation of mass extinctions have followed the same pattern as we saw in Szathmáry's development of major transitions. They call for detailed, complex explanations.

That is, we have on our hands a phenomena-led investigation. Which leads us to ask: what is the benefit of such investigations? Why not simply prefer the theoretical unity and simple narratives of either the original view or a more restricted set of sources (such as transitions in individuality)? I've previously argued that the world's complexity forces us into complex explanations (Currie 2014). Here, I want to say something more positive. I'll demonstrate a crucial advantage of phenomena-led investigation: it allows a wider scope of information to be relevant. As such, I'll

⁵ Indeed, according to Currie (2014) the shift from simple to complex narratives is a common feature of progress in historical sciences.

⁶ I'm unsure whether this context sensitivity is more radical than O'Malley and Powell's proposal.

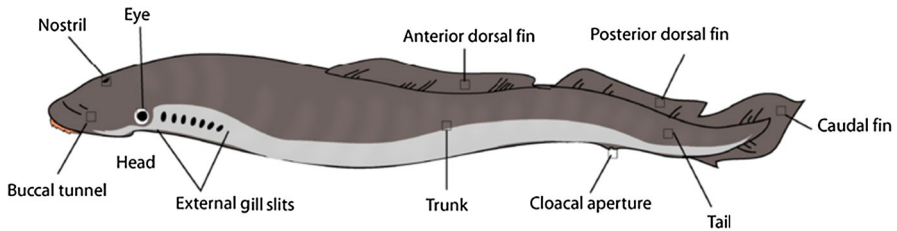


Fig. 1 Lamprey showing unpaired fins (Wikimedia Commons)

argue, it plays a crucial role in the investigative strategies which allow historical scientists to succeed despite the apparent paucity and incompleteness of their evidence. To show this, I want to first consider another set of (perhaps major) transitions of intimate concern to paleobiologists, but traditionally not part of the canon: the evolution of limb morphology. Second, I'll connect phenomena-led investigation to Chapman and Wylie's account of success in archaeology.

Major transitions in paleobiology

I want to claim that phenomena-led investigations are a feature of the strategies paleobiologists adopt when gaining empirical traction on deep time, so it is crucial to see that my point is not restricted to the corner of paleobiology concerning mass extinctions. As such, in this section I want to present another paleontological case study where (1) the investigative target has some claim to being a major transition insofar as it is a biotic event the occurrence of which made a difference to macro-evolutionary pattern, (2) the investigation is phenomena-led. I'll emphasize how the phenomena-led character of the investigation enables the relevance of a vast array of empirical information. This evidential plurality, I'll argue, is a major benefit of adopting a phenomena-led strategy.

Vertebrate paleobiologists often focus on 'organogenesis', the evolution of the vertebrate limb. The transformation from fins to limbs enabled the flourishing of terrestrial vertebrate life; the transformation from forelimbs into wings enabled their taking to the skies. Here, I want to focus on an apparently more humble transition: from median to paired fins. There is a lot to be said about explanations of evolutionary novelty, and the relationship between paleobiology and evolutionary developmental biology, but here is not the place. The point of the example is to demonstrate another paleobiological investigation which is phenomena-led and highlight that phenomena-led investigations maximize evidence plurality.

Agnatha such as lampreys and hag-fishes are extant reminders of the primitive, jawless state from which more derived fish (including ourselves) evolved. These critters sport fins, but they are 'median' fins: lined along the fish's back (Fig. 1).

In derived fish, some fins are paired: instead of aligning along the back, they are partnered and jut out horizontally (Fig. 2).

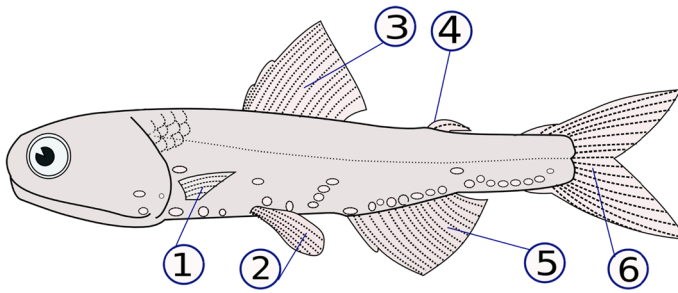


Fig. 2 Hector's Lanternfish with paired pectoral (1) and pelvic (2) fins. Wikimedia Commons

This change is not minor, evolutionarily speaking: “The evolution of paired appendages in the stem gnathostomes enabled more sophisticated control of movement and, subsequently, the development of a diverse array of complex fins and tetrapod limbs” (Sansom et al. 2013). The transition to paired fins, then, was a biotic event which opened up rich new territory for evolution to explore and lineages to take advantage of: a hallmark of a major transition. But how did it occur?

Two hypotheses, both with histories reaching into the nineteenth century (Coates 2003), compete to explain the evolution of paired fins. One takes pectoral fins to have evolved from the gill arch. Gill arches are bony structures which support a fish's gills. On the ‘gill-arch hypothesis’ the posterior-most arch was a precursor to paired fins, gradually evolving a new function. The other, the ‘fin-fold’ hypothesis, notes the existence of lateral ‘folds’ in embryological development, which could have been co-opted for fin development. Both hypotheses provide narratives explaining how paired fins could evolve from the primitive state (what Calcott 2008 has called ‘lineage explanations’) (Fig. 3).

Pieretti et al. (2015) summarize how the hypotheses were first developed in light of embryological studies of sharks, and how “evidence accumulated over the past 120 years has helped evaluate these two hypotheses and assess new fossil, developmental, and molecular data from a variety of species that combine to reveal a third scenario for the origins of paired fins” (4872). They discuss a smorgasbord of evidence. This evidence includes studies of morphological similarity: for instance, the similarity between gill structures and pectoral girdles (which support paired fins) in sharks is taken to favour the gill-arch hypothesis. It includes molecular developmental evidence: Gillis et al. (2009) experimentally demonstrate significant overlap between the genetic controls of fin development and gill development in skates (again supporting the gill-arch hypothesis). It includes evidence from the fossil record: early sharks have a gill structure akin to that of bony fishes, suggesting that current similarities between their paired fins and gills are derived features and thus no guide to their evolution. It includes comparative evidence: a central pillar in the fin-fold hypothesis are the morphological similarities between median and paired fins, making it plausible that the embryological folds which lead to median fins could be co-opted for paired fins.

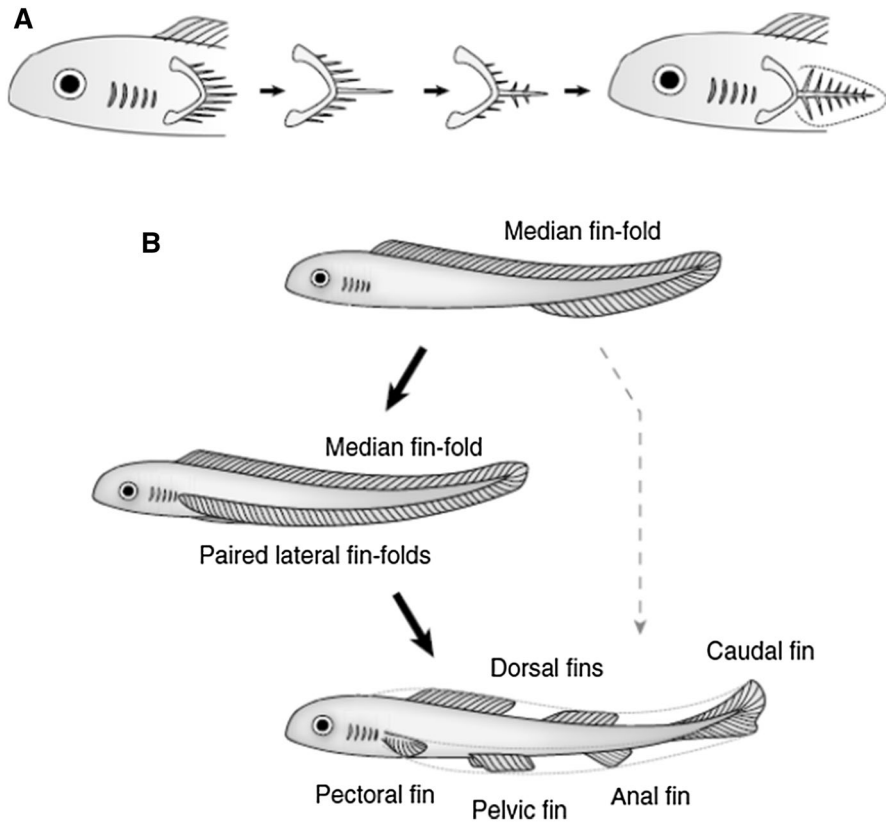


Fig. 3 Two hypotheses concerning the evolution of paired fins. **a** The gill-arch hypothesis. **b** The fin-fold hypothesis (detail from Pieretti et al. 2015, fig 1)

And it includes molecular evidence: phylogenetic trees of extant fish derived from molecular data play a crucial role in framing the hypotheses.

The fossil record is particularly important for informing us about the evolutionary plasticity of the traits in question. Sansom et al. (2013), for instance, discovered a Devonian jawless fish with paired anal fins—a feature not seen before in extant or extinct critters. This potentially suggests a plastic ‘exploratory’ period in early fish fin morphology before the standard bony-fish body plan stabilized. Relatedly, Pieretti et al. report that the fin-folds of early jawed fish are unevenly distributed phylogenetically, suggesting that they are instances of convergent evolution. If fin morphology and development was significantly more plastic in the past than they are now, then identifying a clear path of transformation from basal to derived states is much trickier.

The suggestion that paired fins (of varying kinds) might have evolved many times during this period raises an important question about the nature of major transitions. Major transitions are often taken to be contingent, chancy events which profoundly changed life’s shape. Typically evolutionary biologists take these to be due to the

arrival of a new variant, while at least sometimes paleobiologists blame the pruning of once diverse variants (consider Gould's 1990 suggestion that the chancy survival of *Pikiaia* and the chancy extinction of other critters from the Cambrian made all the difference). However, if paired fins were an event waiting to happen, a 'good trick' given the evolutionary context of aquatic vertebrate-hood, then they may well not have been contingent in that sense. In the spirit of context-sensitivity about major transitions, I won't here commit to whether contingency is necessary for them or not.

Regardless of contingency, this is a beautiful illustration of the opportunism ('methodological omnivorism', Currie 2015, 2018) of paleobiologists: by assaying a wide variety of evidential sources, and adapting knowledge-generating tools to local conditions, they build rich and sophisticated hypotheses concerning the past. More crucially for our purposes, however, this is clearly a phenomena-led investigation. What makes these varied data relevant is not their relationship to some theory, but their relationship to hypotheses specifically pertaining to particular phenomena. Both mass extinctions and organogenesis, then, are clear examples of paleobiologists adopting phenomena-led investigations.⁷ It is time to connect this observation with paleobiological success.

The Paradox of Material Evidence

Alison Wylie has emphasized the capacity of material remains in archaeology to be epistemically transformative: archaeological objects frequently refuse to bow to our theoretical expectations (2002). With Bob Chapman, she develops this as the 'paradox of material evidence' (2016). The paradox emphasises the transience and incompleteness of archaeological evidence on the one hand, and its capacity to be a fulcrum around which archaeological hypotheses turn nonetheless: "... how stubbornly recalcitrant these data can be, no matter how entrenched their assumed meaning..." (Chapman and Wylie 2016, p. 5).

This is a feature of paleobiology too. Although some areas, most notably invertebrate paleobiology, are increasingly marked by large data sets, significant areas of the discipline still remain trace-poor. Yet the capacity of material remains to be transformative is maintained. Under the right conditions, single, incomplete finds can underwrite well-founded, bold claims (such as single mammalian teeth being sufficient to identify hitherto unknown genus, see Currie 2018, chapter 1).

⁷ A reviewer asks whether the conceptual machinery of the major transitions literature has been incorporated into the methodological omnivory of paleobiology. Certainly to some extent: game theory and population genetics have always played a role in paleobiology. Although I haven't looked systematically, my hunch is that this machinery is more often used to highlight explanatory targets for paleobiological investigation than to directly inform reconstruction. For instance, a recent collection on 'major transitions' in paleoanthropology certainly takes the notion in a broad sense (Foley et al 2016). The articles pick out potential game-changers (the use of stone tools, differences in maturation age between *hominids* and close relatives, developmental plasticity, etc...), only a few are plausibly tied to the narrow definition above, and although narrow transitions might frame the discussions, they tend to take a back seat.

Under the right conditions, the discovery of new traces can act as ‘smoking guns’, strongly favouring one hypothesis over another (Cleland 2002, 2011). Like archaeology, it is a *prima facie* mystery how paleobiological evidence, incomplete, biased and degraded as it may be, is able to carry us so far into the past.

Chapman and Wylie resolve the paradox by denying that archaeology has solid, immutable foundations in the sense of their being self-warranting, instead arguing that the foundations of reconstruction and interpretation are provisional and dynamic. The idea is that theory in archaeology doesn’t play the kind of overarching, determining, role that it might in other disciplines. As Wylie says,

Evidential claims may never figure as incontrovertible epistemic foundations, but they do function as a scaffolding, a contingent stopping point in warranting arguments. The question to ask of them is not whether they meet an ideal standard of epistemic infallibility, but how to make best use of the resources at hand to adjudicate their credibility (Wylie 2011, p. 380).

And with Chapman,

Neither these data nor the evidential claims based on them constitute a self-warranting empirical foundation, and yet they can powerfully challenge and constrain the reconstructive and explanatory claims we project onto the cultured past (Chapman and Wylie 2016, p. 6).

In other words, it is *because* there is no ultimate, stable foundation—that the discussion between theory and material remains is dynamic and two-directional—that archaeological (and, I suggest, paleontological) remains are able to speak. Seeing that paleobiological (and, presumably, archaeological) investigations are phenomena-led, I think, deepens Chapman and Wylie’s point.

Phenomena-led investigations are such because the relevance of evidence turns on relationships between phenomena and hypotheses pertaining to them; evidence is relevant to theory-led investigations in virtue of relationship with theory. Theories are often explored and tested by being concretized in simple systems: both computational models and controlled experimental systems (see, for instance, Currie forthcoming). Due to theory’s abstractness and precision, the relevance of actual, longitudinal empirical detail gathered from observations of natural phenomena is often limited. Moreover, the explanations provisioned are, if not ‘how possibly’ than at least concerned with a modal breadth that outpaces the actual history of life, or nearby counterfactuals concerning it. As such, the range of potential evidence pertaining to the phenomena of macroevolutionary pattern differs (and is of a different nature) from the range of potential evidence pertaining to evolutionary theories of individuality and heredity.

There is an asymmetry, then, between theory-led and phenomena-led investigations. Where the latter is of limited value to the former, the lessons, evidence and perspectives of the former are often happily relevant to the latter. We saw this in Szathmáry’s updated discussion of the major transitions: although the explanations have become significantly more detailed and disunified, they have not jettisoned the modelling approaches so constitutive of the original approach to major

transitions. Rather, they are integrated into complex narratives, and supported on the basis of a ‘confluence’ of differing evidence (Currie 2018, chapter 6). Theories, for phenomena-led investigations, do not form a fundamental, unquestioned and unquestionable basis, then, but as Wylie emphasizes, play supporting, scaffolding, and warranting roles.

The upshot of this is that phenomena-led investigations have a potentially larger base of relevant evidence than theory-led investigations. I’m not sure whether this is true in principle, but if the case studies we’ve looked at here are any guide, it is at least frequently the case. Given that paleobiologists and other historical scientists often face limited evidence, and tend to adopt consilience-based, multiple-lines-of-evidence strategies in light of this (Forber and Griffith 2011), phenomena-led investigations are a good strategy as they maximize the amount and variety of evidence.

It is pursuing phenomena-led investigations, then, which enables historical scientists to adopt the opportunistic, pluralistic and methodologically omnivorous strategy which underwrites their success. Further, because phenomena-led investigations treat theory not as a fundamental bedrock but rather place it in a supporting role in helping characterize, evidence and explain target phenomena, they enable the solution to the paradox of material evidence Chapman and Wylie sketch. Material remains are resistant to theory because the structure of paleobiological and archaeological investigation involves provisional theory; it is phenomena-led.

Conclusion

Major transitions are not natural kinds. There is no foreordained set of moments which count as ‘major’ abstracted from investigative context: even if the evolution of paired fins was not game-changing at the scale of the great oxygenation event or the emergence of eukaryotes, it unquestionably changed the game *vis-à-vis* the radiation and history of vertebrates. Indeed, I don’t need to see the history of life as a March towards the apex of humanity to see the mass extinction at the close of the Cretaceous as a momentous event which profoundly affected life’s shape. Which restrictions we should place on the sources and the outcomes of transitions turns in part on what we’re interested in and other features of our investigative context.

I have suggested that much paleobiological evidence is irrelevant to the major transitions literature. This is surprising. You might be wondering: do I want to say that the latter is, properly-speaking, autonomous of the former? Not necessarily. There are some discussions which suggest that paleobiology and neontology ought to be integrated in various ways—for instance that paleobiology deserves a seat at the ‘high table’ of evolutionary theory (Sepkoski and Ruse 2009); while others have suggested that paleobiology and evolutionary theory provide autonomous explanations (Grantham 1999). I’ll close by drawing on Angela Potochnik’s work to sketch a fairly conciliatory relationship between the two.

Potochnik (2010) argues that the optimality approach characteristic of population genetics, and the more mechanistic strategy of evolutionary developmental biology, have independent explanatory goals. Where the former aims to explain how fitter traits become prevalent in a population over generations, the latter aims to explain

how traits might (or might not) arise over evolutionary time. As such, different features matter, and so the details relevant for one purpose can often be black-boxed when pursuing another. I think something similar might be said concerning the relationship between traditional major transitions and mass extinctions. In short, the theory-led questions neontologists ask about macroevolution might have a different explanatory target than paleobiologists considering macroevolution. Accounting for a major transition involves explaining how a population could shift from being a border-line evolutionary individual to a paradigm evolutionary individual. Such explanations are abstracted from, for instance, the extinction events that may have triggered or enabled them (the relationship is not symmetrical, however: explanations of mass extinctions sometimes appeal to theories and models which are the bread-and-butter of major transitions).

However, Potochnik argues that population genetics and evolutionary developmental biology are interdependent epistemically. Sometimes, what goes on in the black boxes matters to whether a particular explanation is true: so, it might be that the applicability of major transition explanations turns on the details of the fossil record. This in itself suggests something about the integration of paleontological evidence and evolutionary theory.

On my view, the major transitions literature, in virtue of the being theory-led, need not incorporate paleontological perspectives into its explanations. However, paleontological data might have an epistemic role to play in constraining and determining the applicability of those explanations to the actual history of life: questions about *when, how, and through what mechanism* transitions have occurred. In answering these questions, it strikes me that paleobiological perspectives, and potentially mass extinctions, are crucial. And I've bet here that investigations of major transitions are shifting into such a phenomena-led key. Perhaps ultimately, whether we think mass extinctions should be counted as major transitions should turn on how that integrative project goes. If it turns out that mass extinction events play a crucial enabling, triggering, or other-wise difference-making role in the occurrence of major transitions, then perhaps their majorness should be taken seriously even by neontological theorists.

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