

Chapter 14

History and Philosophy of Science and the Teaching of Macroevolution

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14.1 Introduction

In the past decade, increasing scholarly attention and emphasis has been placed on the teaching, learning, and assessment of macroevolutionary concepts (e.g., Catley 2006; Nadelson and Southerland 2010a, b; Padian 2010; Novick and Catley 2012). While the distinctions between microevolution and macroevolution have been topics of lively debate within the history and philosophy of science (HPS) communities for some time, relatively new to the field of science education is the conceptualization of macroevolution as a distinct concept in need of targeted instructional emphasis and research (Catley 2006).

The term *macroevolution* is a relatively recent addition to the lexicon of evolution, first coined (in German) by Filipchenko in 1927 and subsequently recruited into the English language in 1937 by the prominent biologist Theodosius Dobzhansky (Burian 1988). Since its introduction, the meaning of the term macroevolution, like many other biological terms, has changed substantially (see Erwin 2010). Despite these changes, nearly all definitions consider the formation of new species to be an important partition dividing micro- from macroevolution. The US National Academy of Sciences (NAS 2012), for example, defines macroevolution as “[l]arge-scale evolution occurring over geologic time that results in the formation of new species and broader taxonomic groups” and microevolution as “[c]hanges in the traits of a

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group of organisms within a species that do not result in a new species.” Importantly, the NAS definitions—and related distinctions in the science education literature (e.g., Catley 2006; Nadelson and Southerland 2010a, b)—focus primarily on *scale* (e.g., within vs. between species; human timescales vs. geological timescales) and *pattern* (e.g., descriptions of large-scale change as opposed to causes of such change). In a similar vein, Catley (2006) highlights the distinction between *short-term* (microevolutionary) and *long-term* (macroevolutionary) change (see also Nadelson and Southerland 2010a, b). While discussions of micro- and macroevolution in the HPS and evolutionary biology literature also focus on scale and pattern, they have paid particular attention to putative factors that *explain* large-scale evolutionary events at different scales of analysis. While natural selection (and other microevolutionary processes) are universally acknowledged as contributors to evolutionary change by biologists, the expansion of possible *mechanisms* accounting for large-scale patterns in the history of life is considered a major advance in evolutionary theory (e.g., Gould 2002). These important distinctions between pattern and mechanism deserve attention, as they have led to a conceptual divergence between the science education and HPS literature.

14.2 Macroevolutionary Patterns and Processes

Macroevolutionary thought has a philosophically rich history (Ruse 1997; Gould 2002; Depew and Weber 1995; Sterelny 2009) and today remains rife with controversy (Dietrich 2010; Erwin 2010). Nonetheless, it is important to point out that many macroevolutionary *patterns* are well established and uncontroversial, such as the reality of mass extinctions (e.g., Jablonski 1986), the originations of now-extinct higher taxa (e.g., Erwin 2010), the evolutionary relationships among all living things (e.g., Hillis 2010), long-term trends in the fossil record (Gould 2002), and evolutionary stasis (e.g., Nehm and Budd 2008). A core macroevolutionary topic of importance to HPS scholars and science educators relates to putative distinctions between large-scale observable patterns in the history of life on the one hand and inferences and theories about the mechanisms responsible for these patterns on the other.

Changes to the definition of *macroevolution* since its introduction in 1927 have in some respects paralleled vacillations between scholarly emphasis on large-scale patterns in the fossil record and their causal underpinnings (e.g., Simpson 1944). Evolutionary biologists from diverse disciplinary backgrounds (e.g., Dobzhansky, Simpson, Mayr, Eldredge, Gould, Gingerich, Futuyma, and Orr) have, like most scientists, recognized that large-scale evolutionary trends, extinctions, and originations of higher taxa do in fact appear in the fossil record (e.g., Simpson 1953; Futuyma 2005; Coyne and Orr 1998; Erwin 2010). But these and many other authors have *disagreed* about whether microevolutionary processes (such as natural selection and genetic drift) are capable of sufficiently accounting for such well-established large-scale patterns (Gould 1985). Causal pluralism, or the expansion of explanatory mechanisms beyond natural selection, is thus a key topic of attention in HPS perspectives on macroevolution. Such plurality is also historically important, as it is

considered by some to be divergent from the views of Darwin (1859), who proposed "...natural selection as the single unifying mechanism that causes both micro- and macroevolution" (Travis and Reznick 2009, p. 126).

Evolutionary theorists such as Filipchenko (1927), Goldschmidt (1940), Schindewolf (1950), Eldredge (1989), Stanley (1980), Vrba and Gould (1986), Lloyd and Gould (1993), and Erwin (2010), for example, have adopted what may be termed a causally pluralistic evolutionary worldview and therein argued that distinct macroevolutionary mechanisms (not reducible to microevolutionary processes; e.g., species selection and mass extinction) likely contributed to large-scale evolutionary patterns (Gould 1985; Erwin 2010). Importantly, these authors do not discount the reality or importance of natural selection, but some have questioned its reification as a causal process with all-encompassing explanatory power (Gould 1981; Depew and Weber 1995). Biologists such as Dobzhansky, Simpson, and Futuyma, in contrast, have generally considered natural selection to be a sufficient causal explanation for most macroevolutionary patterns (for a discussion of Simpson's changing views on this matter, see Sepkoski 2008). The views of these scholars are aligned in some respects with those of Travis and Reznick (2009, p. 128), who note: "In the final analysis there is nothing in the fossil record that inherently contradicts Darwin's daring idea that natural selection is the unifying mechanism." In sum, the reality of macroevolutionary *patterns* is simply not in doubt.¹ The controversy in macroevolutionary biology relates to questions about the *processes* involved (natural selection alone or natural selection+other mechanisms).

According to most definitions, the formation of new species (speciation) lies at the boundary between microevolution and macroevolution (e.g., NAS 2012). While the history of biological thought is filled with controversy about the competing roles of natural selection and genetic drift in speciation, many biologists consider the issue to be settled. Coyne and Orr (2004, p. 410), in their seminal treatment of speciation, note: "...firm evidence for the role of genetic drift in speciation is rare." They go on to close the book on this controversy: "It appears, then, that at least one important debate has been settled: selection plays a much larger role in speciation than does drift. It is also worth noting that genetic drift appears to play little part in morphological evolution" (p. 410). In an exhaustive review of the literature, Coyne and Orr summarize a wealth of work indicating that natural selection plays a major role in speciation and that "[i]t is uncontroversial that most phenotypic divergence in ecologically important traits is driven by natural selection" (p. 385). Thus, natural selection is widely considered to play a major role in the speciation process.

Above the species level, the bulk of macroevolutionary debate relevant to the science education community may be formulated as two related questions: (1) Can microevolutionary processes such as natural selection and genetic drift sufficiently account for large-scale patterns in the history of life? If not, what alternative

¹ Advocates of creationism and intelligent design have repeatedly exploited debates about macroevolution to suggest (incorrectly) that evolution is a theory in crisis and questioned the reality of macroevolutionary patterns because of incompleteness of the fossil record (see Sepkoski 2008). It is important to point out that such incompleteness has not been a topic of equal concern by scientists.

mechanisms are there? And (2) If mechanisms *in addition to* natural selection exist, and they can survive theoretical and empirical testing, how much of the macroevolutionary history of life do they in fact explain (cf. Dietrich 2010)?

Four major macroevolutionary concepts have received considerable scrutiny by evolutionary biologists, paleobiologists, and philosophers of biology over the past 30 years²: (1) species selection/sorting, (2) mass extinction, (3) constraints/evolvability, and (4) evolution and development (or “evo-devo”). The important point to keep in mind is that these four concepts, in concert with (or in opposition to) natural selection, could account for large-scale evolutionary outcomes that were unexpected or unexplainable by the exclusive extrapolation of microevolutionary processes over geological timescales. By expanding the range of causal factors contributing to evolutionary change, evolutionary biologists could potentially improve causal precision and eliminate troublesome empirical anomalies. Questions about the validity of these macroevolutionary processes have generated a rich literature in HPS and evolutionary biology. We briefly summarize each in turn prior to investigating their role in science education.

Species selection has become a key feature of modern macroevolutionary theory (Erwin 2010). It is a conceptual outcome of Eldredge and Gould’s (1972) formulation of evolutionary “stasis” and “punctuated change.” Eldredge and Gould (1972) argued that most species’ histories were characterized by the absence of appreciable evolutionary change (i.e., displayed stasis) and that such stability was punctuated by rapid morphological evolution associated with cladogenesis (lineage splitting speciation) (Nehm and Budd 2008). This model was offered in opposition to what Eldredge and Gould (1972) viewed as the prevailing evolutionary orthodoxy of the time: slow, continuous change. Eldredge and Gould’s alternative model nicely framed the question of whether species could be thought of as *individuals*. That is, in the punctuated model, if species have stability in time and space (a “life span”), and are demarcated by clear beginnings (punctuations associated with “birth”) and clear endings (extinction or “death”), could they not have species-level traits that could be selected, in a way analogous to how individual organismal traits are selected (for the conception of species as individuals, see Ghiselin 1974; Hull 1980)?

Several empirical and philosophical studies of this new conceptualization of species-level selection have been conducted (e.g., Jablonski and Hunt 2006; Hull 1980). These studies generally support the view that species may display properties that are not reducible to lower hierarchical levels, that is, properties that are not aggregates of lower-level phenomena (Stanley 1980; Sepkoski 2008). Geographic range has long been considered a species-level, variable, and heritable trait (Jablonski and Hunt 2006). Philosophers and paleobiologists have debated these empirical cases at length and agree to some extent that species-level selection is theoretically possible (Hull 1980; Sepkoski 2008). Despite being conceptually and philosophically important, so few empirical cases of species selection have been confirmed that the relative significance of this macroevolutionary process appears

²This list is by no means exhaustive (see Ayala and Arp 2010).

to be small (Dietrich 2010). In sum, while species selection may be viewed as a unique and distinctly macroevolutionary mechanism accounting for large-scale evolutionary patterns, the range of phenomena that it might actually explain is quite limited at present.

Like species selection, mass extinctions have been considered to be a central macroevolutionary process (Jablonski 1986). Mass extinctions are important in macroevolutionary thought because they have been thought to cause conceptual complications for extrapolationist accountings of macroevolutionary patterns (e.g., Raup 1994). Mass extinctions have the potential to counteract the smaller scale workings of natural selection; reproductive success and differential survival during “normal” times may have little association with reproductive success and differential survival during times of mass extinction (Jablonski 1986). For example, while patterns of differential survival over millions of years may produce well-adapted animals of large body size, during geologically brief episodes of mass extinction (e.g., the end Cretaceous event), differential survival may favor animals of small body size thereby counteracting this adaptive trend. Mass extinctions therefore raise the possibility that microevolutionary processes alone cannot sufficiently account for large-scale patterns in the history of life (Erwin 2010). The (potentially stochastic) pruning of lineages during mass extinctions may “reset” the playing field for lineages, counteracting the effects of adaptive microevolution. As noted by Raup (1994, p. 6758): “Except for a few cases, there is little evidence that extinction is selective in the [...] sense argued by Darwin.” In this view, natural selection cannot sufficiently account for macroevolutionary patterns; mass extinction must be considered as an additional causal factor that can work in opposition to natural selection.

A third macroevolutionary topic in the HPS literature is constraint and evolvability (Gould 2002; Erwin 2010; Minelli and Fusco 2012). While linking constraint and evolvability is questionable in some respects, both acknowledge the important roles that genetic, architectural, historical, developmental, and functional constraints may play in limiting the types of long-term evolutionary change that can occur (cf. Gould 2002, p. 1059; Erwin 2010). Gould sees particular patterns of macroevolutionary repetition (i.e., parallelism) as evidence of the importance of internal constraints. These constraints are significant in a macroevolutionary sense because they may “push back” against the actions of natural selection and thereby limit pathways of evolutionary change. Put another way, limits on variation (caused by internal constraints) channel pathways of evolutionary change by limiting the options that selection has available to work with. Gould (2002) argues that this perspective is important relative to macroevolutionary theory because constraint helps to explain macroevolutionary patterns that cannot be accounted for by selection alone (see also Bateson and Gluckman 2011 for a more recent discussion). Such views also resonate with many perspectives from evolutionary developmental biology (e.g., Sansom and Brandon 2007; Love 2007, 2013).

Gould’s perspectives align in many ways with the large body of work by Brian Goodwin (reviewed in Goodwin 2009). He challenges the notion that random genetic variation can (or does) generate an infinite variety of options for natural selection to work with, and so natural selection is not the only factor explaining

discrete (vs. continuous) distributions of morphology in time and space. Evidence for this perspective may be found in David Raup's "morphospace" diagrams (see Raup and Stanley 1978). These diagrams map the morphologies of extinct and extant species within the universe of forms that could theoretically exist. Comparing actual vs. possible shell shapes, for example, illustrates that some regions of morphospace are densely populated, whereas others are sparse. Desolate regions of morphospace are fertile ground for exploring the question of whether such forms are impossible to generate or merely have yet to evolve.

Although Erwin's (2010) perspective on evolvability differs somewhat from those of Gould (2002) and Goodwin (2009), it also considers limits on the pathways that evolution can take. Erwin sums up his perspective of "evolvability" when he writes: "...the structure of gene regulatory networks in animals [...] indicates that the nature of the variation available for selection to act upon has changed over time...[and] this may impose another way in which macroevolutionary patterns are not reducible to microevolutionary processes, at least as they are currently defined by microevolutionists" (Erwin 2010, p. 189). He goes on to note "What is strikingly absent from virtually all microevolutionary thought [...] is a sense of history, of the impact of evolutionary changes on the range of variation that is possible, and of how that range of variation has itself changed over time" (p. 191). Thus, Erwin and others have viewed the concept of "evolvability" as a uniquely macroevolutionary idea.

The fourth topic that has received considerable attention in the HPS literature relating to macroevolution is evolutionary developmental biology (informally referred to as "evo-devo") (Carroll 2005a, b). As noted by Raff (2000, p. 74) "evolutionary change occurs not by the direct transformation of adult ancestors into adult descendants but rather when developmental processes produce the features of each generation in an evolving lineage." Although for centuries naturalists have seriously considered the significance of this point (e.g., von Baer 1828; Darwin 1860³; Haeckel 1868; Goldschmidt 1940; Simpson 1944; Schindewolf 1950; Waddington 1970), the role that development has played in macroevolutionary thought has varied dramatically through history (see Gould 1977 for a review). Mayr (1988) argued that development was largely excluded from the "evolutionary synthesis" of the 1940s (see Futuyma 1998 for an alternative view) and subsequently remained somewhat isolated from evolutionary theory (at least in the United States; see Lloyd and Gould's (1993) preface to Schindewolf (1950/1993) for a more global perspective). This situation changed with Gould's forceful reintroduction of the importance of development to macroevolution in *Ontogeny and Phylogeny* (1977). Therein Gould reframed the complex historical literature on evolution and development, crafted a new (largely morphological) framework for

³"Embryology is to me by far the strongest single class of facts in favor of change of forms..." Darwin, September 10, 1860, letter to AsaGray.

heterochrony and heterotopy,⁴ and paved the way for the modern resurgence of interest in evo-devo that has yet to peak⁵ (Carroll 2005a, b).

More recently, the conceptual framework of evo-devo has been further expanded to encompass the genetic underpinnings of largely pattern-based (e.g., heterochrony and heterotopy) changes in the evolution of development. More process-oriented frameworks include heterometry, which refers to an evolutionary change in the amount of a gene product, and heterotypy, which refers to an evolutionary change in the nature of a gene product (Arthur 2004, pp. 81–83). The revolutionary advances in regulatory genetics and genomics has transformed modern evo-devo into a mechanistic science (Carroll 2005a, b). Indeed, the remarkable patterns of evolutionary developmental parallelisms that have fascinated naturalists for centuries are at last being linked to biological processes at the molecular, cellular, and developmental levels (e.g., von Baer 1828; Haeckel 1868; Goldschmidt 1940; Schindewolf 1950; Gould 1977).

Key questions in evo-devo include the study of how gene networks govern ontogeny, the factors that make developing systems robust enough to tolerate mutations that change the course of development, how the rules that govern ontogeny constrain the production of new phenotypic variation, how development influences speciation, and the origins of body plans and their evolvability⁶ (Raff 2000; Arthur 2004; Carroll 2005a, b; Minelli 2009). As noted by Minelli and Fusco (2012): “Overall, developmental processes can contribute to speciation and diversification at different stages of the speciation process, at different levels of biological organization and along the organism’s whole life cycle.” The explosion of empirical findings in evo-devo over the past decade, along with new journals (e.g., *Evolution & Development*), professional societies, and faculty positions devoted to the subject, is suggestive of major changes to the structure of evolutionary biology.

Despite the growing importance of evo-devo for evolutionary studies, and increasing interest in the topic in HPS (e.g., Love 2013), evo-devo has not received concomitant attention in science education research or practice (from the perspective of curriculum or pedagogy; see Love [in press] for a view on both of these issues from a HPS perspective).⁷ Equally concerning is the fact that evo-devo is conspicuously absent from science educators’ recent conceptualizations of the macroevolution construct and associated features deemed worthy of assessment (e.g., Catley 2006; Nadelson and Southerland 2010a, b; see also Novick and Catley 2012). Surprisingly, even Padian’s (2010) vociferous plea for the inclusion of macroevolution in K-12

⁴Evolutionary changes in developmental timing and spatial arrangement, respectively; see Zelditch (2001) for morphological (pattern-based) perspective and Arthur (2004) for a more mechanistic perspective.

⁵The institutionalization of evo-devo took place in 1999 when it was granted its own division in the Society for Integrative and Comparative Biology (SICB), as well as through the National Science Foundation’s establishment of a separate division for funding evo-devo research.

⁶See Müller (2007, pp. 505–506) for a more complete conceptual and historical synopsis.

⁷Although of course there are exceptions. See, for example, a special issue of the journal *Evolution Education and Outreach* (June, 2012).

education lacked explicit mention to the role that evo-devo might play. Thus, evo-devo serves as another example in which current perspectives from HPS have yet to influence the teaching, learning, and assessment of macroevolution.

Our overview of some (but by no means all) of the key macroevolutionary ideas emphasized in the HPS literature—species selection, mass extinction, constraint/evolvability, and evo-devo—and those that have contributed to the resurgence of empirical macroevolutionary inquiry (i.e., the so-called paleobiological revolution of Sepkoski and Ruse 2009) provides a vantage point from which to examine scholarship about the teaching, learning, and assessment of macroevolution in the science education literature. As will become readily apparent, despite some similarities, the two communities have envisioned macroevolution in strikingly different ways.

14.3 Macroevolution: Science Educators' Blind Spot?

Science education research relating to macroevolution has thus far focused on three major issues: (1) general advocacy for the teaching of macroevolution in K-12 education (and cladograms in particular) (Catley 2006; Padian 2010), (2) measurement of students' macroevolutionary knowledge (Dodick and Orion 2003; Nadelson and Southerland 2010a, b; see also Novick and Catley 2012), and (3) investigations of students' beliefs about small-scale vs. large-scale evolutionary change (Nadelson and Southerland 2010a, b). The intrusion of creationist challenges, spurred on by scholarly debates about macroevolution, is also in need of consideration. We begin with a review of advocacy for the teaching of macroevolution in the science education community.

A provocative opinion piece by Kefyn Catley in 2006 was in many respects a “call to arms” for the science education community to acknowledge and explicitly incorporate macroevolution in science education. It bemoaned the lack of focus on macroevolution in science education teaching and research and chastised educators for their near-exclusive focus on natural selection (and associated research on misconceptions about natural selection alone). Catley emphasized that “[w]ithout a clear perspective on macroevolution, an understanding of the full spectrum of evolution is simply not possible. This notwithstanding, microevolutionary mechanisms are taught almost exclusively in our schools, to the detriment of those mechanisms that allow us to understand the larger picture” (Catley 2006, p. 768). In perhaps his most controversial claim, Catley states: “Knowledge of natural selection, while vitally important, explains little about the incredible diversity of species on the planet” (2006, p. 775). Hence, Catley appears to take a stance that is more closely aligned with what we have termed causal pluralism (see above)—that there is more to the evolution of life than natural selection alone. But in addition to natural selection, what, in Catley's view, explains macroevolutionary change?

An interesting aspect of Catley's (2006) perspective is that it lacks mention of the key macroevolutionary concepts (species selection, mass extinction, constraints/evolvability, and evo-devo) that have been central to HPS scholarship (e.g., Sepkoski 2008; Erwin 2010). In fact, it does not clearly outline any causal alternatives to natural selection. This generates a conceptual void: What are we to make of a

“call to arms” for the teaching of macroevolution that downplays the importance of natural selection on the one hand (“By themselves, the products of the “New Synthesis” do not adequately account for the history of life or for its diversity” (Catley 2006, p. 770)) but fails to mention hierarchical selection theory or many of the classic macroevolutionary ideas proposed by Stanley, Gould, Eldredge, Vrba, and Lloyd? If one considers Catley’s (2006) perspective from a pattern-based perspective, however, the exclusion of natural selection, species selection, mass extinction, and constraint and evolvability may be reasonable; students need to learn about large-scale patterns and, according to Catley, learn these patterns through the lens of phylogenetic systematics, or cladistics.

One aspect of Catley’s stance on macroevolution is in alignment with the causal pluralists (cf. Gould 1985). Specifically, he appears to take the position that species are properly conceptualized as “real” individuals (Catley 2006 repeatedly notes that species are “the very units of evolution”). Yet, interestingly enough, he makes no mention of the past 30 years of discussion relating to species selection or how it should be conceptualized in teaching and learning about macroevolution.

A central piece of Catley’s (2006) argument appears to be that cladograms must be integrated into the teaching and learning of evolution and, by doing so, macroevolutionary content will be properly addressed. Cladograms are representational diagrams illustrating the evolutionary relationships of biological units (e.g., species and clades) generated using the underlying methodology of Willi Hennig (i.e., Cladistics; see Hennig 1999). They depict evolutionary *patterns* (characters and their various states across operational taxonomic units, such as species, groups partitioned based upon their recent common ancestry, and outgroups to polarize character state transformations). Cladograms are powerful tools for testing causal hypotheses (such as the “randomness” of mass extinctions), but themselves represent patterns of evolutionary relationship. Therefore, they are tools for articulating patterns in the natural world (the differential birth and death of species within and among clades) with tests of theory (e.g., selection of species in these clades). Macroevolutionary theory and its causal foundations are not necessarily addressed by using or teaching about cladograms (except, perhaps, patterns of cladogenesis), however central they may be to scientific practice. While cladograms have been increasingly employed in evolution research, it is important to point out that the major theoretical advances in macroevolution predated the widespread adoption of phylogenetic taxonomy in the United States (Hull 1988). In sum, while cladograms are now central tools in evolutionary biology, as noted by Catley, by themselves they do not say much about macroevolutionary processes and mechanisms, but only represent patterns.

A recent article by Kevin Padian (2010, p. 206) echoes Catley’s (2006) concerns with teaching macroevolution: “Macroevolution must take a much more prominent place in K-12 science teaching. To do so, a curriculum must be redeveloped at both K-12 and college levels, so that preparation in macroevolution is a required part of K-12 biology preparation.” He also takes aim at his scientific colleagues: “...few evolutionary biologists have a first-hand understanding of macroevolution, and they do not spend substantial time on it in their college courses. This is because most of them are population biologists and population geneticists, and they have had little or no training in macroevolution.” Padian also targets science textbooks: “...textbooks in

all grades from K-16 fail completely to convey an understanding of how evolution works in the long run.”

Catley (2006) and Padian (2010) raise several important points worthy of empirical consideration. First, is macroevolution receiving short shrift in evolution education? Is Catley correct when he claims that “As currently taught, natural selection stops short of fostering an understanding of its effects over time on species themselves, or on cladogenesis. It concentrates almost exclusively on processes that occur within individuals and populations” (Catley 2006, p. 775)? Have aspects of macroevolution in fact been covered in secondary and undergraduate textbooks and curricula? While it is challenging enough today to determine the degree to which particular topics are emphasized in science classrooms, the problem becomes much more difficult to address in the history of science education. One long-standing approach for documenting topical emphasis in the history of science education is to examine textbook content and structure (Cretzinger 1941; Skoog 1969; Moody 1996; Nehm et al. 2009). A surprising number of studies have investigated how evolutionary biology has been conceptualized and represented in textbooks over the past century (for a historical review, see Skoog 1969 and Moody 1996). These studies provide one empirical approach for attempting to answer the relatively straightforward question “Is macroevolution being taught?” Given that Catley’s claim is directed at US education, our review is restricted to that context.⁸

It is clear that many of the concepts that Catley (2006) mentions have been included in biology textbooks in the United States for at least 100 years, although, as mentioned above, this does not necessarily mean that they were covered in classroom instruction. Moreover, it is clear that the term “macroevolution” is a relatively recent addition to the lexicon of evolution, and many texts do not explicitly use this term even if they discuss ideas that are widely considered to be macroevolutionary in nature (e.g., horse evolution). In some of the earliest biology textbooks produced in the United States (from the period of 1900 to 1919), large-scale evolution (between-species change, or transformation) was “...a common topic as it was discussed in five of the eight textbooks” [sampled] (Skoog 1969, p. 151). Other topics present in this early period included “convergent evolution,” “evolutionary relationships,” “fossils and other remains,” and the “evolution of birds” (Skoog 1969). Species transformation again appears as one of the more common topics in textbooks from 1920 to 1929, with the evolution of horses being a particularly common macroevolutionary example⁹ (Skoog 1969). Similar patterns were noted through the 1960s (when natural selection was noted to occur in all of Skoog’s textbook samples; see Fig. 14.1). In a similarly detailed analysis of 17 evolutionary subtopics in early textbooks, Nicholas (1965) found that paleontological evidence from the

⁸While English-language textbooks (particularly from the United States) have received the most attention in the science education literature, it is important to point out that international studies of evolutionary content in textbooks have also been completed. See, for example, Swarts et al. (1994) for a discussion of textbooks from China and the former Soviet Union.

⁹Although one that has more recently been reconceptualized as a branching, rather than as a linear, evolutionary pattern.

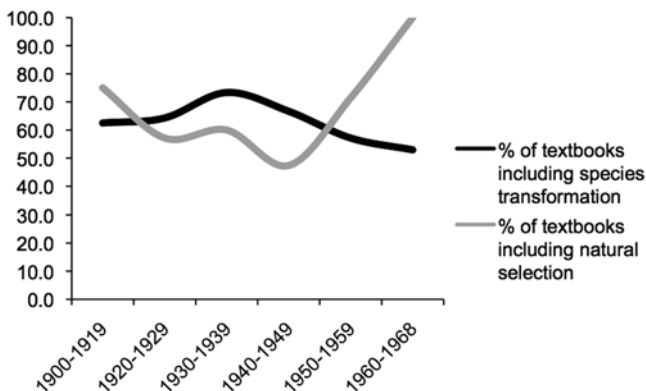


Fig. 14.1 Macroevolution in science textbooks 1900–1968. Based on Skoog’s (1969) analysis of evolutionary content in textbooks from 1900 to 1960, species transformations (macroevolutionary change, according to most definitions; see text) were included at generally comparable levels as natural selection until the 1960s, when natural selection was included in all sampled texts

fossil record was the most commonly covered evolutionary subtopic. Other frequently included topics that could reasonably be considered to have a macroevolutionary slant were “rates of evolution,” “influence of the physical history of the Earth on evolution,” and the “evolutionary history of man [sic].” This work is in alignment with Skoog’s general findings.

More recent studies of best-selling undergraduate biology textbooks revealed that all of them cover macroevolution (Nehm et al. 2009). If the evolutionary history of particular clades is also considered, macroevolution is well represented, albeit segregated to particular chapters (Nehm et al. 2009). Importantly, however, macroevolution is more than tallying long-term patterns of life’s “comings and goings” (Padian 2010); macroevolutionary *processes* are indeed underrepresented in these undergraduate textbooks. In high school textbooks, coverage of macroevolution is difficult to ascertain given that ostensibly macroevolutionary topics, such as punctuated equilibrium, have been lumped with other topics in some empirical studies (e.g., Rosenthal 1985). Nevertheless, it is apparent that many topics that fit under the conceptual umbrella of macroevolution were covered in more recently published textbooks (Skoog 1984; Rosenthal 1985). Given that textbooks “...have much influence on what is taught” (Skoog 1984, p. 127), this finding lends credence to the idea that macroevolution has had a consistent home in biology curricula for a century or more. Nonetheless, it may be true that the proportion of macroevolutionary content is too small (Padian 2010).

The US *National Science Education Standards* (1996) may also be used to examine the status of macroevolutionary ideas in biology education. The *Standards* contain at least ten evolutionary ideas, half of which may be reasonably interpreted as macroevolutionary in nature: (1) common ancestry of species; (2) classification systems reflect evolutionary relationships; (3) the fossil record, large-scale changes in life, and extinction; (4) similarities among diverse species; and (5) geological time, or deep time. Overall, there is remarkable similarity between concepts in the *Standards*

and the macroevolutionary concepts that Catley (2006) and Padian (2010) suggest are lacking in emphasis. Nonetheless, the *Standards* do *not* include the key causal features emphasized in recent HPS scholarship, such as species selection, mass extinction, and constraints on the evolution of form, evolvability, and evo-devo.

In addition to textbooks and the US *Standards*, practitioner journals (such as the widely subscribed *American Biology Teacher*) may be examined to explore the degree to which macroevolution has been addressed in the professional community. Many articles have discussed the importance of teaching both macroevolutionary patterns *and* processes, such as punctuated equilibrium (Alters and McComas 1994); rapid, large-scale morphological and molecular evolution in stickleback fish (Platt 2006); rates of macroevolution (Marco and López 1993); and macroevolution in the fossil record (Dodick and Orion 2003). But on review of the evolutionary topics covered in *ABT*, it is clear that specific macroevolutionary focus is comparatively less than treatments of natural selection and genetic drift. Perhaps the most interesting observation in reviewing the literature is that discussions of *causal* factors relating to macroevolution are extremely rare. So, in many respects, Catley (2006) is correct that macroevolution (at least as HPS scholars' conceptualize the topic, cf. Sepkoski 2008) has received short shrift in science education. But it is also true that facets of Catley's (2006) version of macroevolution are clearly present.

Despite the concerns mentioned above, Catley's (2006) standpoints on macroevolution have without question stimulated a new and innovative research program focusing on student reasoning about phylogenetic and macroevolutionary *patterns* (particularly the interpretation of cladograms) (Baum and Offner 2008). Interpreting cladograms, and using them to reason about evolution (micro- or macroevolution), involves aspects of visual reasoning, hierarchical thinking, abstract representation, misconceptions about evolution, and the nature of science (e.g., cladograms represent testable hypotheses). Given that cladograms have become de rigeur for testing patterns and processes of micro- and macroevolutionary change (e.g., pinpointing likely hosts of the SARS coronavirus, HIV subtype evolution, and the coevolution of angiosperms and their pollinators), this research direction is critically important for the field of science education. What have been lacking in this research program are discussions of the causal *processes* that many HPS scholars consider to be uniquely macroevolutionary, such as species selection, mass extinction selectivity, and clade/group selection (Sepkoski 2008). For some HPS scholars and evolutionary biologists, these ideas form the core of macroevolutionary theory and the most significant conceptual advances since Darwin (Gould 1981, 2002). Yet, it is precisely these concepts that remain conspicuously absent from the science education research literature about macroevolution.

14.4 Measuring Macroevolutionary Knowledge

Given the importance of macroevolution in science education, the question arises as to how to determine if students are learning it. A broad array of empirical research questions in evolution education requires the use of measurement instruments

designed to capture latent constructs, such as students' knowledge of macroevolution or their belief in evolution. In recent years, some science educators have raised concerns about the quality of extant instruments used in science education research in general and evolution education in particular (Nehm 2006; Smith 2010; Neumann et al. 2011). It is critically important that the evolution education research community develops and deploys high-quality instruments that are in alignment with professional measurement standards (i.e., AERA et al. 1999). Otherwise, the measures derived from such instruments will have little meaning, or, more problematically, they may mislead educators in their efforts to improve the teaching and learning of core scientific topics such as evolution. Instruments about macroevolution are no exception.

Nadelson and Southerland (2010a, b) developed the first instrument designed to measure students' knowledge of macroevolution.¹⁰ Several compelling reasons justified the development of this instrument. First, school and university students (and the general public) appear to have different levels of acceptance relating to microevolutionary and macroevolutionary change. Second, many science curricula and textbooks distinguish microevolution and macroevolution as distinct instructional topics (e.g., Stanley 1980). Third, understanding microevolutionary processes (i.e., natural selection and genetic drift) may not translate into an understanding of, for example, larger scale phenomena, such as the formation of new species or evolutionary trends (Catley 2006). Fourth, Nadelson and Southerland (2010a, b) argue that natural selection and adaptation are primarily microevolutionary, and not macroevolutionary, concepts (contrary to the views of some, see above and Table 14.1). Thus, despite several microevolutionary knowledge measures (e.g., Settlage and Odom 1995), a distinct measure of macroevolutionary knowledge appeared to be justified. Given the controversies in the HPS literature about how macroevolution should be conceptualized, to what extent does Nadelson and Southerland's (2010a, b) construct of "macroevolution" align with HPS perspectives?

In designing their instrument for measuring undergraduate students' knowledge of macroevolution, Nadelson and Southerland (2010a, b, p. 156) "...identified deep time, phylogenetics, speciation, fossils, and the nature of science as five essential concepts necessary to comprehend macroevolution." Natural selection is notably absent. The content of the test was established by "...feedback from professional biologists and evolution educators," a review of textbooks, and an expert review revealing that "[e]ach of the five faculty members considered our subscales to be representative of the major topics and concepts associated with macroevolution" (Nadelson and Southerland 2010a, b, p. 156). In one of their open-ended instrument items, they chose to focus on speciation "...because it is often the most contentious concept related to macroevolution" (p. 161). It is by no means clear if HPS scholars would agree that *speciation* is more contentious than, for example, constraints or species selection.

Nadelson and Southerland's (2010a, b) macroevolution instrument uses a "scenario-based" approach, in which students must use information on the assessment to choose among answer options (one scientifically correct, the others

¹⁰ Albeit one that has received considerable criticism. See, for example, Novick and Catley (2012).

Table 14.1 What does the construct of “macroevolution” include? A synopsis of some views from the HPS and science education literatures. See text for details and discussion of causal vs. pattern-based perspectives. Note that discussions in the HPS literature are not explicitly aligned with any educational grade band (n/a)

HPS literature	Padian (2010)	Catley (2006)	Nadelson and Southerland (2010a, b)
Educational level: n/a	Educational level: K-16	Educational level: K-16(?)	Educational level: undergraduate
Natural selection's ability to explain macroevolution (e.g., Gould 2002; Sepkoski 2008)	As a species lineage evolves, its morphology may change in many ways or hardly at all (see discussion, p. 208)	Knowledge of natural selection, while vitally important, explains little about the incredible diversity of species on the planet (p. 775); by themselves, the products of the “new synthesis” do not adequately account for the history of life or for its diversity (p. 770)	Unclear: “... understanding of speciation by natural selection, a fundamental process in macroevolution” (p. 175); “... natural selection and adaptation, which are primarily interpreted as microevolutionary concepts” (p. 155)
Species as individuals; species-level traits (e.g., variability, geographic range); species selection, species sorting, group selection (e.g., Hull 1980; Lloyd and Gould 1993)	The rates of origination and extinction of <i>species</i> shape the history of life (p. 207)	Species radiations, based on novel evolutionary characters; cladogenesis; formation of higher taxa (p. 769); species exist in both space and time, and in addition to being the fundamental elements of Linnaean classification, they are also the <i>units of evolution</i> and biodiversity (p. 775)	Speciation: long-term speciation can be considered to be a key concept that should be included in a measure of macroevolution understanding (p. 158)
Mass extinction selectivity/stochasticity (e.g., Jablonski 1986; Sepkoski 2008)	Extinctions are studied at two levels: background and <i>mass extinctions</i> (p. 208)	Pattern-based extinction (throughout)	Pattern-based mass extinction: diversity of life decreases and increases with events such as mass extinctions (p. 168); an examination of extinction using diagrams of lineages (p. 160)
Constraint, evolvability, and contingency (e.g., Gould 2002; Goodwin 2009; Erwin 2010; Kirschner and Gerhart 1998)	Not explicitly considered	Not explicitly considered	Not explicitly considered
Evo-devo (e.g., Gould 1977, 2002; Raff 1998; Carroll 2005a, b; Arthur 2004; Minelli 2009)	Not explicitly considered	Not explicitly considered	Not explicitly considered

incorrect). Several macroevolutionary patterns are used to frame the instrument answer options: (1) using an evolutionary tree, exploring the *processes*¹¹ involved in the transition of the whale “family” from ancient shore-dwelling ancestors; (2) interpreting the evolution of eyes, including a discussion of variation in extant mollusk lineages; (3) interpreting extinction patterns using “diagrams of lineages”; (4) examining “evolutionary pathways of the African Great Ape” and the development of what they term “diagram pathways”; and (5) interpreting geographic distributions of fossils on different continents. To varying extents, the scenarios test students’ understandings of the five ideas that Nadelson and Southerland (2010a, b) consider to be uniquely “macroevolutionary”: phylogenetics, speciation, deep time, fossils, and the nature of science.

While we suspect that most biologists and philosophers of biology would agree with Nadelson and Southerland (2010a, b, p. 175) when they write, “Assessing learner knowledge of macroevolution is essential for developing and honing science curricula that are effective in helping students develop an understanding of this fundamental aspect of biology,” the discordance between the HPS literature—and other literature in science education—and their concept of macroevolution is notable. In particular, the exclusion of selection and drift as causes of macroevolution (along with the absence of hierarchical selection theory, species selection, constraints/evolvability, evo-devo) are noteworthy gaps. Overall, it is apparent that some science educators are approaching the measurement of students’ knowledge of macroevolution in a unique way, excluding the key features of macroevolution discussed in the HPS literature. The question is whether other education stakeholders conceptualize macroevolution similarly.

14.5 Future Directions in Macroevolution Education

Given the rich literature in HPS relating to macroevolution, it would be useful for teacher educators, instrument developers, curriculum designers, and science education researchers to engage more fully with this work. Our review has revealed several issues that would benefit from a more integrated approach. These include (1) recognizing that natural selection is widely acknowledged to be a major causal process in the generation of macroevolutionary patterns (particularly speciation), that is, constructs of macroevolution should not exclude the theory of natural selection (*contra* Nadelson and Southerland 2010a, b); (2) emphasizing macroevolutionary processes, such as species selection, mass extinction, constraint/evolvability, and evo-devo as core macroevolutionary topics (Table 14.1); (3) developing a consensus definition of macroevolution, associated key standards (i.e., phenomena and processes), and disciplinary practices (i.e., ways of thinking and reasoning,

¹¹ However, no processes (e.g., natural selection, drift, species selection) are offered as answer options on the assessment.

sensu Love 2013) that are appropriate for K-12 students; (4) performing studies of students' knowledge of macroevolutionary phenomena and their reasoning about the processes that might account for those phenomena; (5) linking Catley and colleagues' innovative work on cladogram interpretation with *causal* hypothesis testing. Such work has great potential in integrating a large body of work on microevolution and natural selection with macroevolutionary patterns and causes; (6) exploring how complex system thinking and hierarchical thinking relate to the transfer of natural selection understanding to broader temporal scales; such work is wanting but would add a new dimension to a growing body of work on complex systems (e.g., Wilensky and Resnick 1999). Overall, as envisioned by science educators, macroevolution is a messy amalgamation of phenomena, concepts, and processes united by a weak conceptual framework (e.g., vague notions of "scale"). Currently, the inconsistencies between how the HPS and science education communities envision macroevolution are dramatic, and as a consequence a shared vision of macroevolution is lacking.

14.6 Conclusion

The teaching and learning of macroevolutionary ideas, perhaps more so than other science topics, is tightly bound to the history and philosophy of science (HPS). Nevertheless, as our chapter has illustrated, many studies in evolution education have not fully engaged with HPS scholarship, particularly the topics of species selection, mass extinction, constraint/evolvability, and evo-devo. Currently, science educators' conceptualization of "macroevolution" consists of a messy amalgamation of phenomena, concepts, and processes united by a weak conceptual framework (e.g., vague notions of "scale"). Inconsistencies between how the HPS and science education communities envision macroevolution are dramatic and prevent meaningful progress in the teaching and learning of this important area of evolution.

In closing, after taking stock of the perspectives on macroevolution from HPS, the science education research literature, practitioner journals, and creationist tactics, how should macroevolution be envisioned by science educators and delivered instructionally to students (if at all)? Sepkoski may have provided one of the more reasonable answers to this thorny question when he wrote: "There is no reason to fear teaching schoolchildren that drift, mutation, and natural selection form the central pillar of evolutionary theory, any more than it is dangerous to teach Newtonian mechanics in high-school physics classes. Like quantum mechanics, the current complex debates in macroevolutionary theory are appropriately taught after the basic framework has been established, since they build on, but not invalidate, the foundation" (2008, p. 234). As our review has demonstrated, contemporary views of macroevolution in the HPS community encompass much more than pattern recognition and cladogram interpretation, do not discount the role of natural selection, and offer a more expansive perspective on the range of causal processes that may be responsible for the grand history of life on earth.

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