The Epistemic Value
of the Living Fossils Concept

Aja Watkins*

Living fossils, taxa with similar members now and in the deep past, have recently come under scrutiny. Those who think the concept should be retained have argued for its epistemic and normative utility. This article extends the epistemic utility of the living fossils concept to include ways in which a taxon's living fossil status can serve as evidence for other claims about that taxon. I will use insights from developmental biology to refine these claims. Insofar as these considerations demonstrate the epistemic utility of the living fossils concept, they support retaining the concept and using it in biological research.

Living fossils are taxa in which extant organisms morphologically resemble fossilized organisms; paradigmatic examples include horseshoe crabs, coelacanths, and tuataras. Recently, the living fossil concept has received considerable criticism, contesting even paradigmatic cases. Some argue that the concept is not useful for biologists, since these diverse cases are unlikely to be produced by unified phenomena, while others argue that the concept is useful for certain epistemic and normative purposes. My aim in this article is to address the epistemic value of living fossils, in particular the question: Given that a taxon is a living fossil, what else do we know about it? Using considerations from developmental biology, I show that many common inferences from morphological similarity fail in the context of living fossils. I will argue, however, that there are some inferences that are justified. I conclude that the living fossil concept has epistemic value and, hence, should be retained.

After reviewing recent literature (sec. 1), I address three obvious conclusions that we might draw about living fossils (sec. 2): (1) nonmorphological phenotypic similarity between extant and past taxa, (2) existence of a persistent lineage that includes these taxa, and (3) a slow rate of evolutionary change between these taxa. I evaluate each of these inferences using insights from developmental biology (sec. 3).

*To contact the author, please write to: Boston University; e-mail: ajawatki@bu.edu.

1. Defining 'Living Fossil'. Philosophers have offered different characterizations of living fossils. Lidgard and Love (2018) argue for the concept's usefulness in setting research agendas, despite ambiguity about whether particular taxa are living fossils. Turner (2019) suggests an explicit definition of living fossil, which would allow us to use living fossils to set conservation priorities. Specifically, Turner thinks that living fossils are taxa that have (1) prehistorically deep morphological stability, (2) few extant species, and (3) high contribution to phylogenetic diversity. Werth and Shear (2014) characterize living fossils similarly, picking out "morphological conservatism" and "little taxonomic diversity" as relevant factors (434, 436).

Turner (2019) thinks there is epistemic value to the living fossil concept, including that "observations of [extant organisms in a living fossil taxon] can surely tell us something about the prehistoric ones" (11). The next two sections of this article will specify exactly what we might learn about prehistoric taxa on the basis of their living fossil status. To sidestep debates about the definition of "living fossil," I focus on morphological similarity between past and extant taxa, a feature unanimously associated with living fossils.

I am concerned with whether the living fossil concept is *epistemically* valuable, although it may be valuable in other ways, including for normative purposes (as Turner [2019] argues). I intend to complement, not supplant, these accounts. One area for future research is identifying how the epistemic and nonepistemic uses interact. For instance, Turner thinks that a living fossil taxon's high contribution to phylogenetic diversity has implications for conservation efforts. But we may need to address epistemic issues before we are able to draw appropriate normative conclusions.

The living fossils concept might be epistemically valuable by helping us identify evolutionary episodes in need of explanation, as Lidgard and Love (2018, 2021) argue. In this case, a taxon's living fossil status, or at least the various features associated with that status, is the explanandum. However, in this article, I focus on another possible epistemic role for the living fossils concept: a taxon's living fossil status can serve as evidence for other claims about the members of that taxon.

2. Inferences from Morphological Similarity. To reject the arguments of skeptics who think we should do away with the living fossil concept (e.g., Casane and Laurenti 2013; Mathers et al. 2013; Wagner et al. 2017), we should show what role the concept can play. Lidgard and Love and Turner recognize this, although they have different ideas of what this role is. However, these authors agree that part of what we want to be able to use the living fossil concept for is making inferences from the fact that past and extant taxa are morphologically similar to some other fact F about these taxa. For short:

$$\text{morphological similarity} \rightarrow F. \tag{1}$$

The $\rightarrow$ here should not be taken as a logical relation but merely as indicating that the item to the left of the arrow is evidence for the item to the right.

Both Lidgard and Love and Turner agree that we should be able to use the living fossil concept to make inferences of this form. Turner (2019) calls this the "epistemic value" of focusing on morphological resemblance between past and extant taxa (11).

One fact F that we may want to infer from morphological similarity between two taxa is that these taxa are phenotypically similar in ways above and beyond their morphology. Take horseshoe crabs: extant horseshoe crabs have hemocyanin in their blood (they use copper rather than iron to transport oxygen). Turner (2019) says, "the fossil record does not tell us that ancient horseshoe crabs had hemocyanin in their blood. But that seems like a fairly safe inference, given our background knowledge of phylogeny plus the observation that living ones do have hemocyanin in their blood" (11). The general type of inference that Turner is making is something like

$$\text{morphological similarity} \rightarrow \text{general phenotypic similarity.} \qquad (2)$$

So far, I have been talking about morphological *similarity*, rather than morphological *stability*, the latter of which is used in Turner's definition. Turner (2019) says that morphological stability between past and extant taxa is equivalent to morphological similarity within a persistent lineage (3). If morphological similarity itself were evidence for persistence of a lineage, then morphological similarity would be evidence for morphological stability. Thus, the following inferences are equivalent:

$$\text{morphological similarity} \rightarrow \text{persistence of lineage;} \qquad (3)$$

$$\text{morphological similarity} \rightarrow \text{morphological stability.} \qquad (4)$$

Finally, the living fossil concept may be useful for inferring rates of evolutionary change:

$$\text{morphological similarity} \rightarrow \text{slow evolutionary rate.} \qquad (5)$$

It only makes sense to talk about a rate of evolution within a given lineage. Thus, if the only evidence we have for persistence of lineage is morphological similarity, then inference (3) is necessary for inference (5).

Inferences (2), (3), and (5) do not exhaust the possible inferences from morphological similarity to F that we might make about living fossil taxa, but these examples show the possibility of making inferences about living fossil taxa on the basis of what else we know about them. Thus, these inferences

provide good candidates if we want to demonstrate the epistemic utility of the living fossil concept.

The following section will use some insights from developmental biology to evaluate these inferences.

3. Developmental Considerations. Various concepts and theories in evolutionary biology have been revised in light of results in developmental biology. On the basis of such results, some have even suggested replacing the Modern Synthesis with the Extended Evolutionary Synthesis (e.g., Laland et al. 2015).

In this section, I use results in developmental biology to examine the arguments using morphological similarity from section 2. In each case, I will suggest that we might have thought *antecedently* that these inferences are mediated by genetic similarity. If we thought this, then the inferences would be rather weak, and we might not see much utility in the living fossils concept. However, if we take contemporary developmental biology seriously, we will see that these inferences are not mediated by genetic similarity. In some cases, the inferences are stronger, implying some utility for the living fossils concept.

3.1. Nonmorphological Phenotypic Similarity.   Inference (2) involves inferring from morphological similarity that past and extant taxa have phenotypic similarities above and beyond the morphological ones. For example, we would be able to infer the presence of hemocyanin in past horseshoe crabs from their morphological similarity to extant horseshoe crabs.

One might have thought that the argument relating morphological similarity to general phenotypic similarity implicitly assumed some relationship between morphological similarity and genetic similarity. If morphological similarity were good evidence for genetic similarity, and genetic similarity were good evidence for otherwise phenotypic similarity, then morphological similarity would be good evidence for phenotypic similarity. Including this implicit step, inference (2) would become

$$\text{morphological similarity} \rightarrow \text{genetic similarity} \rightarrow \text{general phenotypic similarity.} \tag{6}$$

Even using a rudimentary understanding of genetics, it is unlikely that inference (6) will work. The problem is that morphological similarity does not imply genetic similarity. There is not, in general, a one-to-one correspondence between genes and phenotypes, including morphology, so we cannot infer genetic information from phenotypic information or vice versa. The same genes can result in different phenotypes, and the same phenotypes can be the result of different genes (e.g., Fusco and Minelli 2010). The former is the

result of developmental plasticity, whereby a variety of environmental factors can affect phenotypic outcomes, for example, by changing gene expression. The latter can be explained by the interchangeability of genes and environment in producing phenotypes, which West-Eberhard (2003) says "conflict[s] with the habit of supposing that the specificity of the [developmental] response comes entirely from the specificity of the gene" (117). If the argument from morphological similarity to general phenotypic similarity depends on an inference from morphological similarity to genetic similarity, the argument will fail, because the first half of inference (6) will turn out to be false. Additionally, and perhaps more intuitively, whatever genetic similarity might be implied by morphological similarity does not in itself imply the additional genetic similarity required to generate phenotypic similarity above and beyond morphology. In the case of the horseshoe crabs, different genes will be associated with morphology than with the presence of hemocyanin.

However, morphological similarity may imply otherwise phenotypic similarity more directly, as indicated in the original inference (2); we might think that certain nonmorphological phenotypes are strongly correlated with particular morphologies.

Whether this correlation is plausible will depend on the nonmorphological phenotype. For instance, whether extant and past horseshoe crabs' blood is similar will depend on whether features of blood are strongly correlated with morphology. If we had independent evidence that the contents of blood and morphology were strongly correlated, then the inference from the horseshoe crabs' morphology to their blood phenotype would be unproblematic. However, as Lidgard and Love (2018) say, "retention of some phenotypic (traditionally morphological) characters does not adequately *explain* change or the lack thereof in other phenotypic characters" (766). Fortey (2011) also thinks that there can be "no final proof" about whether past horseshoe crabs' blood contained hemocyanin (27).

Developmental biologists have recently stressed the *modularity* of phenotypes. This refers to the separability of phenotypes, despite possible integration among them; developmental modules are *semi-independent* and *dissociable*, meaning that traits can occur in different combinations in different organisms, with varying degrees of interdependence between different traits (West-Eberhard 2003, chap. 4). These modules can be selected for separately. For instance, terrestrial and arboreal salamanders have distinct foot morphology; the developmental pathways that lead to these differences are relatively independent from the salamanders' other traits, which go (more or less) unaffected (Gilbert 2000). This is made possible by the branching nature of development: cell differentiation occurs at branching decision points, which are triggered by genetic or environmental switches. West-Eberhard (2019) says that modularity is a "universal property of organismic traits," because this branching process is ubiquitous (357). In the context of living fossils,

modularity means that morphological similarity—which may be dissociable or independent from other phenotypes—does not provide adequate evidence for similarity of nonmorphological traits.

Of course, some modules are more interdependent and can be expected to co-occur. For example, morphology can constrain behavior such that particular behavioral traits are strongly correlated with particular morphological traits. Whether some phenotype provides good evidence for another phenotype depends on having independent evidence of how different developmental modules may be interdependent.

Therefore, the wholesale inference from morphological similarity to phenotypic similarity above and beyond morphology is unlikely to be justified. This is not just a general skepticism about our ability to infer the presence of some traits from the observation of others; developmental modularity gives us good reason to believe that many traits are dissociable. More specific cases, in which a correlation between morphology and other phenotypes is independently established, may allow for appropriate use of this inference in living fossil taxa. Additionally, Lidgard and Love (2018) suggest that one of the questions that research on living fossils might be able to answer is about the role of developmental modularity in patterns of evolutionary stasis (766). In other words, we may come to a better understanding of how different traits are combined in developmental modules by studying stasis of these traits in living fossils.

3.2. Persistence of Lineage.   Inference (3) concludes on the basis of morphological similarity that the taxa are phylogenetically related such that they are both part of the same, persistent lineage or, equivalently, that they are morphologically stable. Neither Lidgard and Love nor Turner make the "lineage" relationship precise. Being part of the same lineage cannot require that the past fossil is an ancestor of the extant organisms, exactly, because we want to permit the past taxon and the extant one having an as-yet-unidentified common ancestor.[1] Nor can the lineage relationship be as broad as a whole clade; it would become meaningless to differentiate living fossils from other cases of relatedness between past and extant taxa. Although it is beyond the scope of this article to more precisely say what a lineage is, it is likely something between an ancestor-descendant relationship and a clade.

Setting this aside: Does morphological similarity imply persistence of lineage or morphological stability? As in the case of phenotypic similarity, perhaps there is an implicit assumption contained in inference (3) involving a relationship between morphology and genetics. Inference (3) could be justified on this basis: if morphological similarity implies genetic similarity,

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1. This is likely the case with horseshoe crabs (Fortey 2011).

and genetic similarity implies the phylogenetic relationship that would hold within a persistent lineage, then morphological similarity would imply persistence of lineage. That is,

$$\text{morphological similarity} \rightarrow \text{genetic similiarity} \rightarrow \text{persistence of lineage.} \quad (7)$$

I argued in section 3.1 that morphological similarity does not imply genetic similarity, so inference (7) will not work. However, we should consider whether morphological similarity implies persistence of lineage without relying on a connection to genetic similarity. There are several reasons to think that it does not; however, morphological similarity is often the best evidence we have of phylogenetic relationships.

First, morphological similarity and persistence of lineage do not imply morphological stability, because of the possibility that the morphological trait was lost and reemerged within the same lineage. Alternatively, if the past and extant taxa are in the same clade but do not have an ancestor-descendant relationship, then it is possible that their common ancestor was not morphologically similar, in which case the morphology would have emerged separately on two branches of the phylogenetic tree, a case of convergent evolution. These considerations when checking for morphological stability are well-known issues with testing for homology (similarity due to common ancestry) in general.

Developmental biologists point out that developmental pathways, even if not morphological traits, may be homologous (e.g., Nijhout 2019, 946). In these cases of parallelism, the trait may appear to evolve separately in two different branches, or may appear to be lost and reemerge, when in fact the mechanism by which the trait develops is actually homologous. We can thus broaden our concept of homology to include parallel evolution and recurrence of traits (West-Eberhard 2003, chap. 25). Doing so accords with Turner (2019), although he does not explicitly use developmental considerations to argue that morphological stability follows from morphological similarity.

Second, though, lack of morphological similarity may not be an indication of lack of morphological stability; polymorphism within a single species is relatively common. Two sample organisms from a species with distinct life stages may be mistaken as organisms belonging to different species if the organisms are observed in different life stages.[2] Species with sexual dimorphism are also liable to be mistaken for multiple species. Both metamorphosis-induced life stages and sexual dimorphism may be the result of developmental modularity (West-Eberhard 2003, 58, 75).

There is thus a risk of false positives and false negatives in identifying persistence of lineage if we focus on morphological similarity. If there were

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2. Turner acknowledges this point (2016, 64). See also Currie (2016).

a better indication of phylogenetic relationships than morphological similarity, we would use it instead.

Nevertheless, morphological similarity is often the best evidence we have for persistence of the same morphology over time, given that in the context of fossils we only have sporadic samples and not any direct evidence of change over time.[3] This is part of the reason why the morphological species concept—rejected nearly unanimously as an adequate concept for extant species—is still used by paleontologists (e.g., Turner 2011, 49–50; Werth and Shear 2014, 442–43). Often the best evidence we have for phylogenetic relationships involving fossils is morphological similarities and differences, and persistence of lineage for living fossils is no exception.

3.3. Evolutionary Rates.   The third inference we might make from morphological similarity within living fossil taxa is a slow rate of evolutionary change between past and extant taxa. The argument for a slow rate of evolutionary change requires that we accept the inference to persistence of lineage. I have suggested that morphological similarity is often the best evidence we can hope to have for persistence of lineage. In this section I assume that that inference is justified and move to examining inference (5), from morphological similarity to a slow rate of evolutionary change.

As in sections 3.1 and 3.2, there is possibly an implicit assumption used here involving genetics. Let us ignore the possibility that the inference looks like this:

$$\text{morphological similarity} \rightarrow \text{genetic similarity} \rightarrow \\ \text{morphological stability} \rightarrow \text{slow evolutionary rate} \tag{8}$$

because we are assuming that morphological similarity is directly evidence for morphological stability (and I have argued that morphological similarity does not imply genetic similarity). In this case, the implicit justification is instead that morphological stability implies genetic stability, which in turn implies a slow rate of evolutionary change:

$$\text{morphological similarity} \rightarrow \text{morphological stability} \rightarrow \\ \text{genetic stability} \rightarrow \text{slow evolutionary rate.} \tag{9}$$

Many of the arguments that morphological similarity will not imply genetic similarity will be arguments against thinking that morphological stability implies genetic stability. I will not rehearse these arguments because there is further reason to think that morphological stability does not imply genetic

3. Our ability to acquire genetic information about fossil specimens may improve our epistemic position regarding phylogenetic relationships, if the inference from genetic similarity to persistence of lineage is better than the inference from morphological similarity (Jablonski and Shubin 2015).

stability. Stabilizing selection acting on plastic traits can maintain the same phenotype over time, without necessarily affecting rates of genetic change. For example, developmental plasticity is expected, especially in cases of extremely plastic traits, to slow any directional increase or decrease in the propensity of a given phenotype in a population, because there is not ample opportunity for selection to act on any single phenotype (West-Eberhard 2003, 178). Furthermore, a process called "phenotypic accommodation" allows organisms to maintain functional phenotypic traits despite genetic mutation (West-Eberhard 2005).

The last step of inference (9)—from genetic stability to slow rate of evolutionary change—is also problematic, although my critique here will be more controversial. Intuitively, a slow rate of evolutionary change in a lineage just is a slow rate of genetic change in that lineage, so the move from genetic stability to slow rate of evolution is unproblematic (e.g., Schopff 1984; Ho 2008).

But is this really what we mean by rates of evolutionary change? Cases of stabilizing selection acting on phenotypes without causing reduced rates of genetic change show that it does not make sense to equate evolutionary change with genetic change. Traits on which stabilizing selection is acting should be traits that we say have a slow rate of evolutionary change: "the rate and degree of modification of a complex trait should be some positive function of its frequency of expression or use" (West-Eberhard 2003, 169). Traits with stability in a given lineage are exactly the traits changing at a slow rate. Therefore, there is no need to appeal to genetic stability to make the case for slow rates for evolutionary change—we can infer slow rates of evolutionary change directly from morphological stability.

It is traits, not lineages or taxa, to which we apply an evolutionary rate. Selection acts on phenotypes, not on organisms, species, or lineages. Lidgard and Love (2018) agree: "characters or character states are relatively more ancestral or derived, not whole organisms or lineages" (761, citing Omland, Cook, and Crisp 2008). Additionally, attribution of rates of change to traits rather than lineages is consistent with the idea of developmental modularity.

One of Turner's examples suggests that he, like me, thinks that morphological stability is a better indication than molecular stability of slow rates of evolutionary change. Tuataras, a reptile from New Zealand, were thought to be living fossils on the basis of morphological stability, until researchers discovered that tuataras have a higher than average rate of molecular evolution (Hay et al. 2008). Some have consequently criticized tuataras' status as a living fossil (e.g., Carnall 2016). Turner (2019) says that even if the study had used nuclear DNA, "developmental processes might insulate morphology from rapid molecular change," and "rapid molecular change in the nuclear genome could also reflect selection pressures on aspects of the organism, like the immune system, that never show up in the fossil record" (14). These

arguments cohere with my evaluation of the inference from morphological stability to genetic stability to slow evolutionary rate. Turner concludes that "in spite of the high rate of molecular change, tuataras are a clear instance of a phylogenetic living fossil taxon" (15).[4]

However, Turner (2019) does not say that we can save the tuataras' living fossil status by appealing to a different idea of evolutionary rates. His reconstruction of the argument against tuataras counting as living fossils is that "living fossils must have especially slow rates of evolutionary change, whereas the molecular evidence points toward especially rapid evolution in tuataras" (14). Turner's criticisms of this line of reasoning challenge the idea that a slow rate of evolution is a necessary feature of a living fossil taxon, rather than the idea that a slow rate of molecular change may not line up with a slow rate of (character) evolution at all. Later, in discussing coelacanths (another candidate living fossil), Turner references "rates of morphological change" but does not equate these rates with rates of evolutionary change (16). Instead, Turner says that "morphological stability in certain characters is entirely compatible with evolutionary change happening under the geological radar" (18). However, as I have argued, morphological stability in certain characters is exactly not compatible with evolutionary change happening on those characters. I suspect that Turner is confusing evolutionary change with molecular change.

Werth and Shear (2014) have a similar take on tuataras. While Werth and Shear do not think that evidence of a higher rate of molecular evolution in this lineage disqualifies it as a living fossil taxon, they say that the high molecular rates "provide strong evidence countering the misconception that living fossils have stopped evolving" (438). Thus, Werth and Shear—like Turner—apparently want to maintain the tuataras' status as a living fossil by arguing that living fossils need not have a slow rate of evolutionary change, rather than by claiming that rates of evolutionary change are best measured at the level of traits, not genes.[5]

A focus on the inference from morphological stability to slow rates of evolutionary change indicates lack of clarity about the epistemic role of evidence for molecular stability in a lineage. Lidgard and Love (2018) say, "the primary role of the living fossil concept is to mark out more precisely what requires explanation in a given instance for a particular entity in order to account for morphological *and molecular* stability or persistence over long periods of evolutionary time" (763, emphasis added). If molecular stability does not

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4. Hay et al. (2008) agree that "rates of neutral molecular and phenotypic evolution are decoupled" (106).

5. Werth and Shear acknowledge that "some biologists speculate that mere genetic change does not translate to evolutionary change" and that there is "independence between molecular and morphological evolution," although they do not endorse this position (2014, 439).

let us infer an evolutionary rate (other than at the molecular level itself), then why might we want to know about molecular stability at all? Lidgard and Love suggest that we might want to know how molecular and morphological rates of change are related or decoupled (766).

The inference to slow evolutionary rates from morphological similarity is the most secure of those I have considered in this article. Interestingly, Darwin (1859/1964) used the term "living fossils" in the context of explaining why some lineages display slower rates of evolutionary change than others. While Darwin's explanation was that these lineages had been "exposed to less severe competition" (107), and now we know that stabilizing selection is more complicated, he still made, by my account, the most reasonable inference from the morphological similarity of extant and past taxa.

The inferences examined in this section are summarized in table 1. In each case, we might have thought that morphological similarity between taxa was only epistemically useful insofar as it implied genetic similarity. First of all, we cannot draw genetic conclusions from morphological evidence. Second, though, the inferences we make about living fossils on the basis of morphological similarity do not require claims about genetic similarity. Indeed, each of these inferences can be made more precise (and sometimes stronger) if we evaluate it in light of developmental biology. This demonstrates the epistemic value of the living fossils concept.

TABLE 1. SUMMARY

Inference	Evaluation
General phenotypic similarity:	
Morphological similarity → genetic similarity → general phenotypic similarity	Morphological similarity does not imply genetic similarity
Morphological similarity → general phenotypic similarity	Morphological similarity only implies phenotypic similarity for some phenotypes (developmental modularity)
Persistence of lineage:	
Morphological similarity → genetic similarity → persistence of lineage	Morphological similarity does not imply genetic similarity
Morphological similarity → persistence of lineage	Morphological similarity does not imply persistence of lineage, but it might be the best evidence we have
Slow evolutionary rate:	
Morphological similarity → morphological stability → genetic stability → slow evolutionary rate	Morphological stability does not imply genetic stability, and genetic stability does not imply a slow evolutionary rate
Morphological similarity → morphological stability → slow evolutionary rate	Morphological stability does imply a slow evolutionary rate, relative to that morphology

4. Conclusion. This article's primary contribution has been to disambiguate the inferences that we can justifiably make on the basis of classifying a taxon as a living fossil, thereby specifying how the living fossil concept is epistemically useful. Specifically, I have argued that lessons from developmental biology can help us to see that some of the inferences made on the basis of morphological similarity between taxa are stronger than we may have realized if we thought that all inferences made on the basis of morphological similarity were mediated by claims of genetic similarity.

This article also serves as an example of how developmental biology can be useful for paleontologists. Historically, development has not been given much consideration in paleontology, largely because fossil evidence does not include information about developmental processes. Discussions of homology, which are relevant to persistence of lineage, involve the contributions of both paleontologists and developmental biologists. Living fossils serve as another example of the productive combination of developmental biology and paleontology, using evidence about fossilized as well as living taxa. The arguments in this article may have other implications for paleontology outside of the context of living fossils and more generally point to the fertility of exploring the intersection between developmental biology and paleontology.

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