The living fossil concept: reply to Turner

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Abstract

Despite the iconic roles of coelacanths, cycads, tadpole shrimps, and tuataras as taxa that demonstrate a pattern of morphological stability over geological time, their status as living fossils is contested. We responded to these controversies with a recommendation to rethink the function of the living fossil concept (Lidgard and Love in *Bioscience* 68:760–770, 2018). Concepts in science do useful work beyond categorizing particular items and we argued that the diverse and sometimes conflicting criteria associated with categorizing items as living fossils represent a complex problem space associated with answering a range of questions related to prolonged evolutionary stasis. Turner (*Biol Philos* 34:23, 2019) defends the living concept against a variety of recent skeptics, but his criticism of our approach relies on a misreading of our main argument. This misreading is instructive because it brings into view the value of three central themes for rethinking the living fossil concept—the function of concepts in biology outside of categorization, the methodological importance of distinguishing parts and wholes in conceptualizing evolutionary phenomena, and articulating diverse explanatory goals associated with these phenomena.

Keywords Conceptual role · Living fossil · Part-whole · Research program.

Despite the iconic roles of coelacanths, cycads, tadpole shrimps, and tuataras as taxa that demonstrate a pattern of morphological stability over geological time, their status as living fossils (LFs) is contested (Gall and Grauvogel-Stamm 2005;

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Nagalingum et al. 2011; Casane and Laurenti 2013; Cavin and Guinot 2014; Mathers et al. 2013; Herrera-Flores et al. 2019; Vaux et al. 2019; Johnson 2020). Most of these disputes turn on whether and how to categorize an item as a living fossil. At issue is the assumed priority of different kinds of characters that are used to represent an item (e.g., specific mitochondrial or protein coding genes in contrast to key morphological characteristics or overall morphology), and whether this choice alters or upsets inferences about evolutionary rate or duration.

We responded to these controversies with a recommendation to rethink the function of the LF concept (Lidgard and Love 2018). Concepts in science do useful work beyond categorizing particular items (Brigandt 2010; Brigandt and Love 2012). We contend that a LF concept plays a role in setting a research agenda in evolutionary biology. Specifically, we argued that the diverse and sometimes conflicting criteria associated with categorizing items as LFs represent a complex problem space associated with answering a range of questions related to prolonged evolutionary stasis. In doing so, we advocated for the explicit recognition of parts as defeasible proxies for wholes to better differentiate distinct questions, evaluate the kinds of data most relevant to answering these questions, and articulate the standards of adequacy associated with providing empirically robust answers. Our analysis was both interpretative and normative. It offered an interpretation of existing research on entities categorized as LFs and provided counsel for how to understand and frame this research going forward.

Turner (2019) defends the LF concept against a variety of recent skeptics who have advocated restricting its application or urged its outright elimination. He recognizes that we are allies in defending an ongoing role for the LF concept in opposition to critics but disagrees with us on the preferred strategy. However, Turner's defense and criticism of our approach relies on a misreading of our main argument. This misreading is instructive because it brings into view the value of three central themes for rethinking the LF concept—the function of concepts in biology outside of categorization, the methodological importance of distinguishing parts and wholes in conceptualizing evolutionary phenomena, and articulating diverse explanatory goals associated with these phenomena.

This restricted construal stands in contrast to our more pluralist recommendation to rethink the LF concept as a broad research agenda that is inclusive of a wide range of phenomena and interrelated questions. Moreover, Turner's stance could be interpreted as introducing a measure of arbitrariness, however well-intentioned. A LF taxon, according to Turner's PLF concept, exhibits: "(a) Prehistorically deep morphological stability; (b) Few extant species; [and] (c) High contribution to phylogenetic diversity" (5). It is not clear why this particular set of criteria that "sometimes co-occur in ways that are theoretically and practically interesting" (3) are privileged, whereas other individual criteria or clusters of criteria that have been well-established across biology are not. From our perspective, Turner's version of LFs is well motivated by conservation concerns and the definitional criteria he offers fit within a broad LF research agenda. Yet this fit obtains *alongside of and complementary to* many other LF phenomena, criteria, and questions that scientists obviously do "care about." A conception of LFs motivated by conservation concerns does not require abandoning these other concerns, many of which may similarly "push back" against

critics skeptical of the LF designator. In fact, some researchers explicitly adopt this viewpoint: “we do not aim to give a new definition for ‘living fossil’... Rather, we use phylogenetic and conservation approaches to propose *a more specific concept in biodiversity conservation*, namely ‘endangered living fossil’ (ELF)” (Vargas et al. 2020, 2, emphasis added; see also Bond et al. 2020).

We begin this discussion note with a brief historical review of LFs followed by a restatement of our argument in order to highlight areas of agreement and disagreement with Turner’s formulation. We agree with Turner that a LF concept has value in epistemic as well as normative senses. In addition to resisting skeptics and offering ways of understanding the LF concept for research on various biological questions, we also concur that conservation priorities are a part (though not the whole) of the LF research program and that clusters of criteria can facilitate the operationalization of the concept methodologically. However, instead of offering objections to our central themes, Turner’s analysis represents a nascent exemplar of the type of research program that we explicitly recommend but without giving attention to the methodological distinction between parts and wholes, and without considering how his PLF concept would fit into, rather than displace, a broader LF research agenda. We believe these oversights handicap his otherwise illuminating account.

Historical context

The historical trajectory of concepts is crucial to understanding their current use and value. We concur with Turner that “scientific concepts such as “living fossil” have histories; they get put to work in different ways, and for different purposes, at different times” (5). However, the history appealed to by Turner is more complex than he envisions. For example, he claimed that the platypus was anomalous for Darwin because it seemed to be intermediate between mammals and reptiles. (A generalization of this example is recruited to support Turner’s own use of the LF label.) However, the notion of “intermediate form” operative in Darwin’s time was more variegated, in part because of competing schemes of classification vying for acceptance, such as Jussieu’s natural method or the quinary systems of Macleay and Swainson (Ospovat 1981; Novick 2016, 2019). Textual evidence of Darwin’s thinking about the relationship between LFs and anomalous or aberrant morphology reveals both change and ambiguity. Darwin had begun engaging with Macleay’s work by the early 1830s (Novick 2019), including the quinary notion of “osculant types,” which referred to taxonomically intermediate forms with affinities that “linked” different but otherwise adjacent larger groups of taxa (though not in the same evolutionary sense that would emerge in Darwin’s published theorizing). By postulating a temporal dimension to quinary schemes, Darwin initially accepted Macleay’s osculant forms as LFs, often having few species and looking anomalous or aberrant (i.e., not morphologically typical of other genera closely associated in the classification).

This view shifted from the early 1840s onward as Darwin investigated the idea that diverse genera had broader geographic ranges and were better adapted to competitive “external conditions” than species-poor genera with smaller ranges, which

were vulnerable to extinction. Darwin began looking at aberrant groups as LFs by virtue of the extinction of allied genera. However, such aberrant groups were not necessarily intermediate and transitional between other, larger groups (Ospovat 1981). Corresponding with Joseph Hooker in 1858, Darwin wrote: “Thus I explain the fact of so many anomalous or what may be called “living fossils” inhabiting now only fresh-water, having been beaten out & exterminated in the sea by more improved forms; thus all existing Ganoid fishes are fresh-water as is *Lepidosiren* & *Ornithorhynchus* &c. ...” (Darwin Correspondence Project, Letter 2384). While the platypus *Ornithorhynchus* and the lungfish *Lepidosiren* lacked a fossil record and were seen as intermediates (at least in taxonomic classification) by Richard Owen before 1859 (and by many others long after), this was not true for ganoid fishes (genera including gars and bowfin with characteristic bony and enamel armored scales). Agassiz had defined the main groups of fishes on the basis of their scales, with ganoids and placoids going back in time to the earliest known fossil-bearing strata without a clear sense of being intermediate between other major groups (Jameison 1835). In various letters and notes before and after 1859, Darwin alludes to or names other taxa as living fossils—cave-dwelling insects, the salamander *Proteus*, *Amblyopsis* fishes, the gnetalean plants *Gnetum* and *Welwitschia* (and arguably others). These had little to no role as transitional intermediates, making this particular LF criterion ambiguous and suggesting a less restrictive conception.

Concepts in biology often transform and sometimes broaden over time (Love 2015; Brigandt 2020), and this has been the case for the LF concept. Bernard Lapepède, a prominent French zoologist who held transformist views, “came very close to the notion of living fossil” around 1800 by comparing fossil and extant forms, including fishes and cetaceans (Schmitt 2010, 447). Decades before *On the Origin of Species* (Darwin 1859), deep-water marine dredging yielded sensational discoveries of living representatives of ancient, long-extinct fossil lineages abundant in the “secondary formations,” including crinoid echinoderms and the bivalve *Trigonia*. In the latter half of the nineteenth century, the idea that the deep sea was a refuge for LFs flourished, and the drive to establish genealogies of aberrant types became a major focus of research that continues today (Mayr 1985; Ramirez-Llodra et al. 2010). This recognition overlapped in perception—if not always in name—with a broadening scientific awareness and concept of LFs (Rudwick 2005, 2008; Etter and Hess 2015). By the early twentieth century, *Ginkgo* (known to Darwin as *Salisburia*) was commonly styled as a LF, “a survivor of a race which has narrowly escaped extinction” (Seward 1911, p 126). Discoveries and scientific reception of the coelacanth and the “primitive” mollusk *Neopolina*, both widely hailed as LFs, vividly recall the earlier discoveries of living crinoids and *Trigonia*. The larger theoretical context has grown in many respects since Darwin’s time and has been elaborated through consideration of more possible items as LF candidates. We contend that it is a mistake to think there is only one way to conceive of LFs and that Darwin’s usage simply differs from our own or that he was interested in transitional forms, but we should instead concentrate on “ethical and aesthetic interests in biodiversity” (Turner 2019, 6).

Another aspect of historical transformation is seen in the operational breadth of the concept, including what kinds of items biologists have considered as LFs.

Fig. 1 Living fossils in biological publications. **a** Estimated trends among named taxa (species, genus, family, higher taxon) and non-taxonomic objects (biomolecule, virus or viroid, organelle, other). **b** Estimated trends in repeated occurrences of some canonical living fossil taxa in biological publications over the past fifty years. Data are raw counts over five-year intervals from searches of Google Scholar using the terms “common name OR scientific names (species, genus, family)” plus “living fossil.” We retained only publications in which the author(s) provided justification of why a biological item was a LF. Each scientific name appears only at its earliest occurrence in the data. Different taxonomic ranks are counted separately (e.g., genus *Ginkgo* and species *Ginkgo biloba*)

Turner’s defense of a PLF concept restricts it to items “above the species level.” A core element in our argument is that the label “living fossil” is applied to many biological items. Evaluating them commensurately is not trivial. To explore possible historical trends in biologists’ focus on LF items, we compiled Google Scholar search results for the terms “living fossil(s)” and “year” over the past century, adding relevant titles from bibliographies (mainly from English-language biological publications—see Fig. 1 legend for details). Our data compilation is far from complete but is intended to document general trends rather than exact numbers. Beginning with Ruedemann’s (1917) list of persistent, relatively unchanging taxa under the term “arrested evolution,” virtually all of those that survived to the Recent have been considered LFs by subsequent authors. Although genera are most prevalent (Fig. 1a), the label has been applied repeatedly—with explicit justification in biological publications—to species, families, higher taxa, organelles, and biomolecules. We wholeheartedly agree with Turner that we are not testing different definitions of LFs against our intuitions; many people would not consider the LF moniker applicable to a protein (Hantke 2003; Schuldiner 2014).

Researchers in diverse subdisciplines—biochemistry, physiology, molecular genetics, phylogenetics, conservation, and others—are investigating taxa and their morphological or molecular parts precisely because they are LFs, by whatever definition. This fact coincides with another argument for retaining a broad-sense LF concept—its usefulness beyond specific claims of the normative purpose of LFs: “a

taxon's living fossil status can serve as evidence for other claims about that taxon" (Watkins 2020, 1).¹ If we are trying to understand scientific reasoning, then we need more than conservation priorities or the particular constellation of morphological features exhibiting evolutionary stasis associated with PLFs. Otherwise, we will miss the theoretical and practical importance of the LF concept. The PLF concept overlooks what scientists care about that is not above the species level and many epistemically important avenues of research. When Turner argues that, "I've shown here, however, how to resolve much of the ambiguity in a relatively straightforward way" (17), he neglects to mention how much removal of conceptual behavior was required to accomplish this intended clarification.

One final historical remark is warranted. Turner states that the LF concept has "fallen on hard times." We concur that there has been a marked increase in questioning the status of certain canonical LFs in recent years, particularly in studies using biomolecular data to infer phylogenetic relationships and evolutionary rates. Yet this observation does not tell the whole story. Recent high-profile discussions of LFs are also positive (Zhao et al. 2019; Johnson 2020). Biologists invoke LFs as a focus of research ever more frequently (Vargas et al. 2020) and increasingly employ canonical LFs (Fig. 1b), regardless of associated controversy and often without conservation biology in view. In particular, patterns of striking "conservation" (homology) in molecular sequence or functionality are a form of evolutionary stasis that earns the LF label (Zhu et al. 2005; Schmitz 2012; Wang et al. 2014). There is no doubt that the PLF concept can be helpful in countering some recent criticisms. However, what it cannot do is illuminate the full range of reasoning contained in the LF research agenda, including questions about many patterns in need of explanation and processes relevant to our understanding of evolutionary stasis across hierarchical levels of organization.

Living fossils as a research program

Our reanalysis of the LF concept and its function in biology took as a point of departure the routine use of the LF label across disparate areas of research and the worries about it generating misleading inferences that had provoked skepticism of its value. We advanced two central themes to accomplish a rethinking of the concept and its functional roles: (1) the need to move beyond categorization, and (2) the methodological value of distinguishing parts and wholes. With respect to the former, we highlighted the diversity of prominent criteria that have been used to identify entities as LFs in evolutionary biology:

- Prolonged geological duration relative to similar entities
- Slow rate of evolutionary change relative to similar entities
- Gross similarity to an ancestral fossil

¹ "Insofar as these considerations demonstrate the epistemic utility of the living fossils concept, they support retaining the concept and using it in biological research" (Watkins 2020, 1).

- Very low taxonomic richness today compared to the past
- Relic geographic range today compared to the past
- Phylogenetic inference of specific characters as ancestral
- Phylogenetic inference of a genealogical divergence between other groups that diverged in the distant past
- Known in the fossil record before being discovered alive

We think these criteria mark something significant, something that encourages a broader rethinking of LFs and leads to a different view of the concept. Biologists often steer clear of definitional debates as unproductive, but these debates typically presume that the primary role of a concept is to ascertain which set of entities should be classified by a particular term. Yet scientific concepts also play a role in representing broad investigative domains—in biology, terms like “gene” and “fitness” have repeatedly provoked debate over their ranges of meaning and measurement at different times and in different contexts (Brigandt 2010; Abrams 2012). However, these concepts continue to serve as useful organizing notions and are operationalized diversely across research contexts. The LF concept typically marks out what requires explanation in a given instance of morphological or molecular stability over long periods of evolutionary time. Different conceptions and criteria of LFs derive from different explanatory expectations and empirical progress (e.g., increased sampling of the fossil record) that change how the conceptions apply. This rethinking directly addresses skeptical complaints about the concept, such as cross-cutting definitional criteria or preservation biases in the fossil record.

Another big idea—the value of distinguishing parts and wholes—is related to the routine use of proxies or measurements of particular properties that stand in for something else. An awareness of this methodological distinction can lead to empirical progress. For instance, part-whole ambiguity (P-WA) is significant in relation to a common practice: single size and shape characters are taken to represent a species or lineage in most quantitative paleontological studies of evolutionary modes (Hopkins and Lidgard 2012). Although this common practice has been fruitful because these single characters sometimes serve as useful proxies, analyses where multiple characters are recorded for fossil populations of the same species or lineage in successive stratigraphic levels over geologic time frequently distinguish different evolutionary modes for different characters (Hopkins and Lidgard 2012; Hunt et al. 2015; Voje et al. 2018). Depending on the characters chosen to represent a lineage as a whole, the trajectory detected over geologic time can be quite different from a trajectory detected using a different character or set of characters. Taxa exhibit a mix of morphological and molecular components, and often there is a complicated relationship between parts and wholes through evolutionary time.

We maintain that recognizing P-WA and putting it to use can be productive in analyses of diverse kinds of research questions related to LFs. Moreover, as noted, distinct criteria that had been used to *categorize* LFs can be deployed singly or in combination to *elucidate* what is in need of explanation for specific questions. Different criteria need to be made explicit in different contexts and in relation to other allied questions to explain slow or negligible rates of evolutionary change for constellations of molecular or morphological characters in genealogical lineages. The

result of combining an explicit recognition of complex part-whole relationships with distinct explanatory roles for different criteria is a LF concept that can be understood as setting a broad agenda for research. This agenda is composed of interrelated suites of questions about patterns in need of explanation and processes relevant to specific character constellations and wholes. Addressing these questions advances our understanding of evolutionary stasis within and across hierarchical levels of organization.

To help illustrate our formulation, consider a specific research question: “Why do some living fossils exhibit “relic” geographic distribution (i.e., a distribution that is significantly more restricted than in the geologic past)” (Lidgard and Love 2018, p 767)? If we ask whether a taxon is geographically widespread, then we are tracking wholes—organisms and their lineages. However, if we talk of a LF “retaining” an ancestral morphology, this retention often concerns particular characters or parts that may be relevant to its distribution. The characteristic leaf form of *Ginkgo* has long been used as evidence of its extraordinary geological persistence since the Jurassic, “perhaps more venerable than that of any other forest tree” (Gardner 1883, 45). *Ginkgo* has inspired a massive ongoing research enterprise exploring its iconic role as a geographic relic (Fig. 2), with fossil and phylogeographic analyses using morphological (leaves) and molecular characters. *Ginkgo*, *Cercidiphyllum*, and a few other genera were once widespread in the Northern Hemisphere but became confined to Eastern Asia near the end of the Cenozoic. Cenozoic co-occurrence of *Ginkgo* and *Cercidiphyllum* in disturbed streamside environments suggests prolonged conservation of their habitats, but finer-scale studies revealed incongruent episodes of retreat, colonization, and expansion linked to changes in preferred habitats (Zhao et al. 2016). *G. biloba*’s more restricted, disjoint distribution relative to *C. japonicum* may relate to longer generation times, more climatically vulnerable reproductive periods, or more limited dispersal of its fleshy seeds compared to wind dispersal (Zhao et al. 2016), implicating population demographic and life-history traits as potential explanations. All of these patterns are derived from conserved fossil and modern morphological parts, particularly leaves, that stand in as proxies for species wholes. A partial re-analysis of these patterns based on genetic characters using phylogenetic analyses and evolutionary rate estimation examined the sustained survival of *C. japonicum* and *C. magnificum* (referred to as LFs and relics) through a Miocene speciation event, an early Pliocene divergence of Chinese and Japanese populations, and range expansions and contractions through interglacial cycles (Zhu et al. 2020). They infer increasing population sizes over much of these lineages’ histories, with relatively late fluctuations in response to severe climatic swings. In their estimation, this inference challenges, “the oft-stated view of relative demographic stasis in ‘living fossils’” (10), and that reduced genetic polymorphism through late population bottlenecks was mediated by long-term balancing polymorphism and population sweeps associated with local adaptation. We view these divergent part-whole perspectives that utilize contrasting morphological and genetic proxies for lineage wholes as providing complementary insights about LFs (Hoban et al. 2019).

This and other research questions correspond to one or more of the cross-cutting membership criteria that make the LF concept contentious. Thinking explicitly about relationships between parts and wholes requires revisions in how we understand

Fig. 2 Eocene to Recent geographic occurrences attributed to the canonical living fossil *Ginkgo*. The overall patterns demonstrate a dramatic reduction in geographic range. Approximate latitude–longitude coordinates were assigned to published *Ginkgo* fossil localities based on Shaparenko (1935), Kovar-Eder et al. (1994), Uemura (1997), Dillhoff et al. (2005), references therein and subsequent citations. Occurrences are based on preserved morphological parts, predominantly leaves. **a** Eocene and Oligocene fossil localities. **b** Miocene and combined Pliocene and Pleistocene fossil localities. **c** Recent “natural” relic populations of *Ginkgo* are controversial due to historical human intervention. Putative survival population areas shown here are from the molecular genetic phylogeographic analysis of Gong et al. (2008)

some stereotypical LFs but also makes sense of the complex discourse surrounding them. Our account consolidates a broad array of heterogeneous and fragmented investigations, provides a framework that steers clear of semantic debates, and facilitates interdisciplinary research on evolutionary questions surrounding molecular and morphological stasis.

Misunderstanding the project

We contend that Turner misunderstands the main argument of our paper. He says: “They [Lidgard and Love] are skeptical about the possibility that any living fossil concept can do a good job of sorting taxa into those that count as living fossils and

those that don't" (Turner 2019, 12). We argued that no subset of criteria for LFs will do a good job of sorting *all* of the taxa *and other entities* that many researchers think should be counted as LFs. However, this argument has a larger purpose—to show that categorizing is not the only or the primary conceptual role of interest to focus on. Thus, when Turner says further that, "They would be right, if there were no principled reasons for zeroing in on particular criteria" (12), he actually confirms our point. The principled reasons for zeroing in on some subset of criteria for what counts as a LF reflect commitments to particular evolutionary questions of importance in the research program about the stability of a trait, cluster of traits, or wholes through time. We suggest that Turner's mistake is thinking there is only one way to do this (his PLF concept) and for positing the primacy of just one reason (conservation of taxa). We agree that "there are compelling theoretical and (especially) practical, normative motivations for defining "living fossil" in a particular way" (9); we simply do not think only one particular way fits the bill, and no argument has been given for why we should expect this. There are compelling reasons that motivate pursuing diverse evolutionary phenomena and questions about LFs, which can be better understood as elements of a research agenda where conservation-related questions comprise a viable subdivision.

Turner might not recognize the main point of our argument because he misunderstands our target. He wants to justify the LF concept by appeal to the need to defend LF taxa ("The best way to defend the concept of living fossils is to get clearer about the reasons for defending living fossil taxa" [1]); we want to justify the LF concept by appeal to a different picture of how concepts operate. Turner thinks he can win the definitional debate ("I tackle the definitional issue head-on" [3]); we suggest a different focus—what concepts do—is more descriptively adequate and practically fecund. Turner assumes there is a unitary fact of the matter about whether a taxon is a LF; we argue that many things have been and can be categorized as LFs, and this is done on the basis of facts about stasis that are diverse and yield cross-cutting classifications. The best bet for defending LF taxa is to better understand how the LF concept works in scientific practice.

The irony is that our picture includes his strategy as one among many that are possible. He claims that our argument "makes no contact with conservation biology," (3) which is only true in the sense that we did not discuss it explicitly among several other illustrative examples (Lidgard and Love 2018). However, our account of the LF concept as a research program fully embraces conservation biology as one of its dimensions, and aesthetic value as a possible basis for intervention. Turner argues that the PLF concept is favored by normative considerations, such as environmental, ethical, or aesthetic values. These provide a justification for the three criteria that Turner thinks "really matter": (a) prehistorically deep morphological stability; (b) few extant species; and (c) high contribution to phylogenetic diversity. That these criteria "really matter" with respect to some normative considerations is eminently reasonable; we are persuaded that phylogenetic diversity is an important form of biodiversity worth preserving (e.g., Bennett et al. 2019). However, we also think these criteria could be justified via non-normative considerations. For example, as Turner recognizes, his cluster of three criteria might direct our epistemic attention to particular taxa that can be explained similarly, independent of any non-epistemic value

commitments (“Why do the three features of phylogenetic living fossils sometimes co-occur?” [9]). More generally, other sets of criteria can be justified by a variety of descriptive and normative considerations. We agree with Turner that “there are reasons why existing taxa that have these features should be prioritized for conservation efforts” (3), but not that this justification is unique or the only legitimate basis for a LF concept.

Parts, wholes, and the tasks of criteria

Our emphasis on P-WA in the original argument was intended to demonstrate that what is often conceived as a source of criticism for the LF concept—breadth of applicability—is actually a way of recognizing one of its strengths. This moves us beyond definitional worries about a category with vague boundaries and provides a route to both clarify and advance research. Although we never claimed that P-WA was the only issue of importance, Turner’s argument for the PLF concept provides us with further illustration of its significance.

In order to operationalize a given LF conception, one or more criteria are put to work. Then evidence is required to determine whether a relevant condition or set thereof has been met. Evidence may involve properties of wholes (e.g., species richness or geographic range of a genus or family) or properties of parts (e.g., morphological or genetic characters as proxies). With regard to Turner’s PLF criteria, we first ask whether these properties are most relevant to answering a particular question, and whether they articulate the standards of adequacy needed for empirically robust answers. His first criterion, “prehistorically deep morphological stability,” relates to properties of parts, but without further detail P-WA can enter in several ways. “Prehistorically deep” could be measured by molecular or morphological phylogenetic distance, time of origin estimated using molecular clocks, or origin based on observed occurrence of key morphological characters in the fossil record. These measures need not agree (e.g., Nagalingum et al. 2011; Cavin and Guinot 2014). The same sort of disagreement could arise depending upon which genes or morphological characters are chosen. Similarly, “morphological stability” is subject to P-WA in regard to determination of which characters, how many, and using what sort of method and relevant level of adequacy.

Another instance of P-WA in Turner’s analysis relates to the taxa that characters are embedded in: “The phylogenetic living fossil concept does not imply species stasis, but only character stasis. All that’s needed is that certain morphological traits exhibit long-term stability” (7). The PLF concept specifies only entities above the species level, but there are lots of stereotypical structures within a lineage that are stable at one hierarchical level but variable at another. Assuming a specified subset of morphological characters has privileged status and exhibits long-term stability does not by itself answer which taxa (and taxonomic rank) they are embedded in without some implication of stasis. There also is no reason to hold that external body morphology is the only relevant trait. The “horseshoe crab body plan” appears twice in Turner’s discussion but may not be a well-defined basis for characterizing morphological stability (cf. Wray and Strathmann 2002). He maintains that

“morphological stability is a matter of degree” and is related to the descriptive grain used to individuate traits. Turner is willing to grant that “if one describes the traits at a coarse enough grain—focusing, perhaps, on the tetrapod body plan—then the lineage leading to humans exhibits just as much morphological stability as horseshoe crabs” (8). This would make sense only if there were explicit criteria that guided the appropriateness of grain for trait descriptions in particular research contexts.

The other criteria need further detail to avoid P-WA. “Few extant species” requires a standard for how many will be needed to meet the assumed threshold when there are large population numbers for a few extant species as opposed to small population numbers for a few more extant species. The latter seems highly pertinent to conservation priorities and therefore, unlike what Turner claims, relict groups are not so easily distinguishable from LFs (Nagalingum et al. 2011; Bennett et al. 2019). “High contribution to phylogenetic diversity” can pertain to either morphological or genetic parts. The phylogenies that undergird assessments of evolutionary distinctiveness are themselves subject to P-WA since parts serve as proxies in phylogenetic reconstruction as much as they do in discriminating species and measuring morphological stability in the fossil record. And, as Turner recognizes, there is disagreement about what “should be included in a measure of evolutionary distinctiveness” (7). Prioritizing evolutionarily distinct species is still a largely untested supposition (Bennett et al. 2019) and different quantifiable factors should be considered (see also Morelli and Møller 2018).

Not recognizing P-WA leads Turner into empirical difficulties for PLFs. He routinely moves between parts and wholes in empirical cases. Tuataras are analyzed with respect to their rate of molecular evolution and skeletal morphological stasis. The high rate of the former is discounted in evaluating its status as a LF (“developmental processes might insulate morphology from rapid molecular change” [14]), but the latter is emphasized based on “lower jaw morphology” [15]. As noted, different choices of parts as criteria in either instance may alter the perceived outcome (Gemmell et al. 2020; Herrera-Flores et al. 2019; Vaux et al. 2019). In his discussion of cycads, Turner first treats the entire exterior morphology of one Triassic fossil species, *Holozamites hongtaoi*, “that looks just like a sago palm, a kind of modern cycad that many people keep as houseplants” (13), as an exemplar of morphological stability for cycads in general. Then he appeals to molecular phylogenetic estimates as showing a Neogene radiation of living cycad species—estimates based not on whole organisms but on a sampled part, the nuclear gene *Phytochrome P* (see also Salas-Leiva et al. 2013; Condamine et al. 2015).

In reviewing morphological differences between extant and extinct coelacanths, Turner notes overall body length, different skull morphologies, and fin symmetry versus asymmetry. What is missing are explicitly delineated reasons why these are traits diagnostic of taxa or why their differences are more important than other similarities. What counts as significant morphological change depends on the part that is used as a proxy for the whole. Turner concludes that “morphological disparity and change in the Paleozoic and Mesozoic coelacanth fossil record is actually compatible with morphological stability over the last 60–80 million years,” but “whether you “see” morphological stability in coelacanths depends a lot on which traits you choose to measure” (16). We agree—this is the issue of P-WA. It affects not only

the assessment of LFs but also phylogenetic comparisons of uniquely derived traits in hummingbirds, perch, and coelacanth to ascertain relative rates of morphological change. Turner's goal of using his PLF concept to both resolve ambiguity and defend a circumscribed set of LF taxa cannot succeed without further specification to address questions related to P-WA.

Conclusion

Turner's PLF account seems to raise as many questions as it answers and misses "much of what scientists care about" when labeling entities as LFs. Only when we recognize a difference in the role played by the LF concept can we understand both why there are skeptics (because of cross-cutting criteria that yield different categorizations depending on the research question) and why the LF concept continues to sustain a research program (because there is a range of questions related to prolonged evolutionary stasis of different entities). Once recognized, it facilitates paying closer attention to methodological issues of how parts are proxies for wholes in paleontological and other analyses pertinent to questions about LFs. This turns our attention to both specifying the kinds of data most relevant to answering these questions and articulating explicitly the standards of adequacy that determine when accounts are explanatory. The LF concept—both in the past and even more so in the present—is multifaceted and theoretically rich because it corresponds to an ongoing research program in evolutionary biology. It includes biodiversity considerations based on aesthetic values but is by no means exhausted by them.

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Compliance with ethical standards

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