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# Editorial: New perspectives on living fossils

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Editorial on the Research Topic
New perspectives on living fossils

## Hesitation: the controversy

What is it about "living fossils" that triggers dissatisfaction among scientists? The concept has been criticized for ill-defined definitional criteria, molecular genetic change despite apparent morphological stasis, faulty phylogenetic inference, or inadequate measurement of evolutionary rates (Schopf, 1984; Bennett et al., 2017) in groups as dissimilar as cycads (Nagalingum et al., 2011), tadpole shrimps (Mathers et al., 2013) and coelacanth and polypterid fishes (Casane and Laurenti, 2013; Near et al., 2014). Complaints generally concern whether to categorize a biological entity as a living fossil. The hesitation from these concerns does not tell the whole story and is not a reason to forsake analyses of living fossils. Instead, what matters is whether the living fossil concept can be used constructively. Our argument is that concepts have a role in science beyond categorization (Lidgard and Love, 2018; Lidgard and Love, 2021). Routine usage of a living fossil concept reflects a research agenda on evolutionary stasis, consisting in a set of interrelated questions contextualized to serve particular explanatory tasks (Lidgard and Kitchen). What we need is to use our concepts wisely. Here we summarize how papers in this Research Topic exemplify this pattern of wise use and consider the challenge of utilizing the concept moving forward.

## Appreciation: the papers

The first thing to appreciate is just how routinely the living fossil concept is invoked. Lidgard and Kitchen capture the expansion of criteria from 1860 through the present, tracing the ongoing increase of over 800 entities named as living fossils across kingdoms and the biological hierarchy, from RNAs to taxonomic Classes. No single definition adequately describes all contexts and named entities. Rather, within a research agenda, distinctive living fossil criteria are most appropriate for a given question and particular entity (or entities). Turner and Han show that many proposed definitions appeal to a distinctive evolutionary history and this provides a foundation to ascribe conservation value to living fossil taxa. Vargas analyzes endangered monotypic genera, applying an "Endangered Living Fossil"

concept pragmatically to prioritize specific taxa for conservation. Two papers address conflicts that arise when one set of traits seems to challenge living fossil status and a different set appears to support it. This requires thinking in terms of parts and wholes (Lidgard and Love, 2018): when should sets of traits like genes or morphological structures be considered proxies for historical entities like species or genera that bear them? Analyzing the Hox gene cluster in branchiopod crustaceans, Nicolini et al. show how morphological evolution is not tightly associated with genome dynamics. Rieppel elegantly traces systematists' recognition of the mosaic evolution of characters in a lineage back into the late 19th century; its occurrence in living fossils does not differ from other taxa. Instead of part-whole conflicts disqualifying a living fossil concept, the contrasting signals can be scrutinized to understand how and why they occur, and why rates of change seem so disparate. Cavin and Alvarez provide evidence that suggests long generation and gestation times help to account for the slow rate of evolution in the coelacanth body plan. Sterner grapples with operationalizing criteria for living fossils by comparing two theoretical frameworks as a basis for improving evidential standards for classification. Finally, Hopkins et al. question whether there is anything special about the present time in pursuing living fossil questions—can "extinct living fossils" yield valuable new insights?

## Utilization: the challenge

The primary challenge for any scientific concept is how it use it. "A concept is only as good as the research program it inspires … concepts should play the role of inspiring and guiding progressive empirical and theoretical investigation" (Wagner, 2015, 340). This challenge involves at least three tasks: explicit characterization, research question articulation, and the specification of evaluative standards. First, given different living fossil criteria, no researcher should assume their use of the concept is implicitly understood. If you intend "living fossils" to pick out prolonged geological duration relative to similar entities, then explicitly characterize what counts as prolonged duration and which entities are relevantly similar for comparison. If you intend "living fossils" to pick out very low taxonomic richness today compared to the past, then explicitly characterize what counts as high and low taxonomic richness and what past junctures should be used for comparison. Similar situations arise with scientific concepts such as "gene" or "species."

Second, articulate the research question with precision. If you are considering why some but not all constellations of morphological characters exhibit apparent stasis over long periods of time in the same lineage, delineate which constellations of morphological characters are in view and how you would adequately measure their properties to test different hypotheses. Some research questions appear similar but require asking something distinct. The recurring problem of how suites of morphological versus molecular characters are related to slow rates of change (if at all) is not identical to the first question, because discrepancies in evolutionary rates between groups of morphological characters do not yield immediate answers to discrepancies in rates between a group of morphological characters and a group of molecular characters.

Finally, it is crucial to specify evaluative standards for a concept, especially when used across different disciplinary approaches. For example, if the aim is to draw a phylogenetic inference about specific characters being plesiomorphic, then the relevant evaluative standards derive at least in part from phylogenetic methodology. The ability to ascertain whether a living fossil entity represents a retention of ancestral character states cannot rely on presumptive inferences about the characters of unstudied species or use pruned trees for comparison (Jenner, 2022). The specification of evaluative standards means that one can incorrectly invoke the idea of a living fossil, whether for the purpose of categorization or evolutionary inference. A combination of explicit characterization, research question articulation, and specification of evaluative standards facilitates progressive empirical and theoretical inquiry.

Although more can be said about how to operationalize the living fossil concept within a research program about stasis—slow or negligible rates of evolutionary change—for diverse features in living systems, the contributions to this Research Topic display the productivity we should expect of a scientific concept and thereby offer exactly what was intended: new perspectives on living fossils.

## Author contributions

SL and AL contributed equally to conception of the idea for this Research Project, working with authors and reviewers, and writing the editorial. All authors contributed to the article and approved the submitted version.

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Publisher's note



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