Book Review

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What do paleontologists mean by "species"?

Allmon, Warren D., and Margaret M. Yacobucci, editors. 2016. **Species + speciation in the fossil record.** The University of Chicago Press, Chicago, Illinois. vi + 427 p. $65.00 (cloth), ISBN: 978-0-226-37744-5 (alk. paper); $65.00 (e-book), ISBN: 978-0-226-37758-2.

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Paleontologists and neontologists both make generalizations about species. However, it's not always clear that they are using the term "species" in the same way. Paleontologists typically have nothing to go on but morphology. Does this mean that they should work with a morphological species concept? Or should they instead take morphology as *evidence* of species membership, while relying on some other account of what species are, such as the popular biological species concept? That sounds reasonable, until you think (for example) about cryptic species—cases where reproductively distinct species have nearly indistinguishable morphologies. To make matters even more complicated, processes of speciation often seem to fall through the cracks of our evidence base. Speciation is usually too slow to observe in real time. But it often happens too fast to show up very clearly in the geological record. So what exactly should "species" mean in paleontological contexts? And how might patterns in the fossil record contribute to our understanding of the processes of speciation?

The fourteen papers collected in *Species and speciation in the fossil record* approach these issues from a variety of different directions. Five of the papers focus on issues specific to different taxa: coral reefs (Budd and Pandolfi, Chapter 7); ammonoids (Yacobucci, Chapter 8); lobsters and crabs (Schweitzer and Feldmann, Chapter 9); echinoderms (Ausich, Chapter 10); and fishes (Bemis, Chapter 11). Historian of science David Sepkoski helps to frame the issues by offering a look at early efforts by paleontologists such as G. G. Simpson and especially Norman Newell to think about species as they worked to clarify paleontology's place in the Modern Synthesis (Chapter 1). The contributions by William Miller, III, and Warren Allmon (Chapters 2 and 3, respectively) take on the species problem from a paleontological perspective. Especially interesting is Allmon's defense of the general lineage concept of species (or GLC), proposed by Kevin de Queiroz, and not too far removed from Simpson's evolutionary species concept. Allmon defends the GLC partly on the grounds that it would enable paleontologists and neontologists to avoid talking past one another. In a similar spirit, Allmon and Sampson (Chapter 4), defend a four-stage conception of speciation that they hope will help to unify discussions in paleontology and neontology. Steven Hageman (Chapter 5) connects the discussion of species and speciation with one of the big issues in paleontology today—namely, how to integrate molecular and morphological data. Lee Hsiang Liow and Torbjorn Ergon (Chapter 6) develop a mathematical model for representing the relationship between speciation rate and the age of a taxon. Is it, for example, easier in some sense for species to speciate when they are relatively new?

Species and speciation in the fossil record is a rich collection that will prove valuable to anyone interested in theoretical paleobiology, in the species problem, or in the challenge of understanding macroevolution. The last three papers in the volume are especially noteworthy, and I want to say a bit more about them here.

First, Alycia Stigall (Chapter 12) summarizes research on two fascinating cases of prehistoric biological invasions: the Late Devonian biodiversity crisis and the Late Ordovician Richmondian invasion. One thing that makes these case studies interesting is that both involved significant drops in speciation rates. Stigall argues that there are some patterns that repeat in both cases: Biological invasions are accompanied by selective extinction of ecological specialists. But because ecological specialists tend to have higher speciation rates, that means that speciation rates fall. So what you end up with is a mix of native generalist taxa and generalist invaders—"cosmopolitan species"—that have big geographic ranges. Although I admit that the normative baggage attached to the term "invasive species" makes me uncomfortable, Stigall's research might offer an important rejoinder to recent writers like Fred Pearce (2015), who seem to think that we should not lose any sleep over invasive species at all. On the contrary, and setting terminological qualms to one side, the fossil record suggests that biological invasions can depress speciation rates, thereby having a big impact on biodiversity even if they don't cause many extinctions.

Second, Melanie Hopkins and Scott Lidgard (Chapter 13) draw a connection between the themes of the volume and the issue of stasis in the fossil record, an

issue that has received a lot of attention since Eldredge and Gould (1972) first argued that stasis is the dominant theme of evolutionary history. But Eldredge and Gould's idea is vulnerable to a circularity problem: If paleontologists treat morphological similarity as the criterion of species membership, then their very method of organizing fossils into species could generate the appearance that species do not change (much) morphologically once they first evolve. Hopkins and Lidgard try to cut through this problem in an ingenious way. They start by looking at studies aiming to identify patterns of stasis (as opposed to directional change or random walks) in the fossil record. Then they cross-check to see whether the traits used in those studies are *also* used to identify fossil species in phylogenetic studies. They find that "a majority of the traits that show directional change or a random walk are taxonomically useful, while a slight majority of traits that show stasis are not useful or unused" (p. 376). This result somewhat alleviates the worry about circularity. For if circularity were really a problem, one would expect a stronger correlation between the traits that are useful for delimiting fossil species and those that exhibit stasis.

Finally, Prothero and colleagues (Chapter 14) present some of their research on the remains of animals (wolves, bison, horses, camels, big cats, and birds) from the Rancho La Brea Tar Pits in California. They are also exploring the relationship between neontology and paleontology in an interesting way. Consider a neontological generalization such as Bergmann's rule, which describes what might be called a "geocline": When you have a species with a large geographic range, individuals in the colder parts of that range will tend to have larger body sizes. Does this rule also describe a "chronocline"? That is, if temperatures cool over time, will body size tend to increase? The La Brea Tar Pits offer a way to test this, because they record a period during which there were several climatic shifts. Surprisingly, the fauna of the tar pits exhibit a high degree of evolutionary stasis in spite of those climate shifts, and contrary to what Bergmann's rule would lead us to suspect.

One might wish for more engagement with the vast literature on the species problem in the philosophy of biology. And one topic that gets surprisingly little attention in this volume is species selection, which is clearly related both to the species problem and to the study of differential speciation rates. Nevertheless, *Species and speciation in the fossil record* is an extremely valuable resource for anyone interested in conceptual and theoretical issues in paleobiology. The volume offers an excellent window on how paleobiologists today actually think about species.

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