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Betting & Hierarchy in Paleontology

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In his *Rock, Bone, and Ruin: An Optimist's Guide to the Historical Sciences*, Adrian Currie argues that historical scientists should be optimistic about success in reconstructing the past on the basis of future research. This optimism follows in part from examples of success in paleontology. I argue that paleontologists' success in these cases is underwritten by the hierarchical nature of biological information: extinct organisms have extant analogues at various levels of taxonomic, ecological, and physiological hierarchies, and paleontologists are adept at exploiting analogies within one informational hierarchy to infer information in another. On this account, fossils serve the role of building necessary epistemic connections between different hierarchies; consequently, Currie's optimism about future research outcomes should be limited by optimism—or a potential lack thereof—about future fossil discoveries.

Part of an author-meets-critics book symposium on Rock, Bone, and Ruin: An Optimist's Guide to the Historical Sciences (*2018, MIT Press*) *by Adrian Currie, with Adrian Currie, Alison Wylie, Joyce C. Havstad, and Derek Turner*.

1 Introduction: The Bets We've Won

At the turn of the last century, paleontologists wagered that they could find the missing link between lobe-finned fish and early terrestrial vertebrates. Given how these evolutionary relatives are distributed in the fossil record, Daeschler et al. (2006) predicted that some transitional form awaited discovery in late Devonian outcrops of the Canadian Arctic. It was there that they won their bet: the team soon found *Tiktaalik roseae*, a "fishopod" with a mix of aquatic and terrestrial traits. *Tiktaalik*'s discovery now stands as paleontologists' textbook case of scientific reasoning done right (Benton 2014, 88–96).

Daeschler et al.'s story is one about hope fulfilled. Their optimism is hardly unique among paleontologists: we can tell similar stories about discoveries of the ancestors of whales (Madar

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and Thewissen 1994) or the earliest known shelled turtles (Li et al. 2008). Given how many stories of fulfilled hopes that paleontologists can cite, one might argue that paleontologists have good reason to be optimistic. Indeed, that is precisely Adrian Currie's point in his 2018 *Rock, Bone, and Ruin: An Optimist's Guide to the Historical Sciences*.

Currie argues that "methodological omnivory" is the basis for optimism in historical sciences such as paleontology. Given how paleontologists mix and match successful methods used elsewhere, they are likely to find their own success in reconstructing the past. Among these successes, Currie recounts examples such as research into sauropod gigantism, saber-tooth bite mechanics, and the evolution of echinoderm development. These cases provide further compelling evidence that paleontologists should be optimistic about their collective ability to reconstruct the past.

Nevertheless, paleontological optimism is warranted only in a limited range of cases. These cases are unified by their exploitation of points of overlap between different biological hierarchies (cf. Eldredge 1991). Where paleontological inference requires ranging beyond these points of overlap—in particular, where fossils do not show us the range of hierarchical overlap—paleontologists remain pessimistic. For all the success that paleontologists have found, fossils serve as a check on paleontologists' exuberance.

2 The Argument against Pessimism

Currie (2018, 13) argues in favor of what he calls predictive or epistemic optimism. This is optimism about research outcomes: "the optimist predicts that we will often succeed" in attempts to reconstruct the past. By contrast, epistemic pessimists doubt that historical scientists can reliably reconstruct the past. By denying a reasonable basis for pessimism, Currie concludes that paleontologists (and other historical scientists) can be justifiably optimistic.

To motivate his optimism, then, Currie must explain why historical scientists such as paleontologists might be pessimistic. Citing arguments from Gee (2000) and Turner (2015) among others, Currie (2018, 8) notes three recurrent themes in historical pessimism. First: historical evidence is relatively rare. Second: the rarity of historical evidence tends to increase as information degrades over time. Third: the increased rarity of historical evidence cannot be mitigated by the manufacture of contemporary facts. Conjoining these three ideas—we don't have much information, we're losing what we do have, and we'll never get it back—should diminish our confidence in paleontologists' ability to reconstruct the past; hence paleontological pessimism.

The structure of Currie's argument for optimism in the historical sciences—and, thus, paleontology—is (perhaps ironically) polemical. Against the first two pessimistic themes, Currie argues that historical scientists can turn to contemporary analogues as evidence for historical patterns and processes. Against the third pessimistic theme, Currie argues that historical scientists can use simulations and models can generate evidence that decides between competing historical theories. To summarize: we do not actually have good reasons for pessimism and so we should be—and often are—optimistic.

I will focus here on two of Currie's examples. In the first example, a variety of contemporary analogues suggest the function of saber-teeth in the marsupaliaform predator *Thylacosmilus atrox*. In the second example, digital models explain macroevolutionary patterns in echinoderm development. These examples undermine the argument for pessimism; I will show that they also mark the boundaries of optimism.

Thylacosmilus, an extinct, pouched mammal from South America that resembled saber-toothed cats, is the subject of one of paleontology's many success stories (Currie 2018, 214–222). Paleontologists' success in reconstructing the form and function of the animal's saber-teeth came

in spite of research taking place in an "unlucky" context. The context was "unlucky" in Currie's (2018, 131–135) sense of being relatively information-poor. Paleontologists have recovered few *Thylacosmilus* fossils and so the animal's evolutionary relations remain mysterious. Furthermore, neontology offers no extant saber-toothed predators for comparative research. Nevertheless, this lack of clear analogues did not prevent Wroe et al. (2005) from inferring that *Thylacosmilus* used its saber-teeth to kill already-immobilized prey and not as a means of subduing prey. This conclusion followed from a chain of comparisons, first between modern cats and saber-toothed cats and then between saber-toothed cats and *Thylacosmilus* itself. This stepwise accumulation of indirect evidence mitigated the paucity of direct fossil data.

Research into the evolutionary transition between extinct and extant echinoderms is another example of paleontologists' success in an information-poor context (Currie 2018, 231–235). In this case, the lack of data was a function of the target system in research. Developmental differences mark a clear distinction between modern echinoderms and their extinct relatives, but the mechanisms that underlie differences in development do not fossilize. Nevertheless, Zachos and Sprinkle (2011) mitigated the lack of fossil evidence by modeling different hypothetical manipulations of modern echinoderms' developmental system. One particular manipulation yielded simulated echinoderms that strongly resembled extinct forms, thus implying that a similar developmental shift lies in Echinodermata's evolutionary past. As Currie puts it: "models compensate for missing data" (232).

Currie is effective in his use of these examples to demonstrate the failure of pessimism in paleontology. In both cases, pessimists had voiced their doubts and were subsequently silenced. Nevertheless, there is one salient similarity between these examples that limits Currie's optimism.

3   The Limits of Optimism

Information in the life sciences is hierarchical. This is true not only in taxonomy, but also in physiology and ecology. These hierarchies overlap at various levels: organisms straddle the physiological and ecological hierarches, for example, while species are a connection point between the taxonomic and ecological hierarchies (Eldredge 1989, 185–200). Consequently, information in each level in a particular hierarchy implies some range of information in other hierarchies. These points of inferential connection explain how paleontologists were successful in the cases given above.

Paleontologists overcame "unlucky" circumstances in studying *Thylacosmilus* and extinct echinoderms by recognizing appropriate points of connection between hierarchies. Organisms that occupy the same level of the ecological hierarchy share relevant physiological similarities between them, regardless of their places in the taxonomic hierarchy; Wroe et al. could therefore make inferences about *Thylacosmilus* from ecological analogues despite the absence of contemporary taxonomic analogues. In the case of echinoderm research, Zachos and Sprinkle took advantage of higher-order similarities between all members of the taxon Echinodermata to draw physiological inferences about extinct forms. These inferences from one hierarchy to another show why paleontologists should be "methodological omnivores," as Currie (2018, 157–161) suggests: they often borrow the tools for studying one hierarchy to study another.

Similarly, hierarchical overlap explains why paleontologists find themselves in "unlucky" research contexts. "Unlucky" circumstances are those in which the range of inference from one hierarchy to another is relatively limited. That *Thylacosmilus* and modern leopards occupy similar levels of the ecological hierarchy implies some physiological similarities, but not others. Information about predatory physiologies—bite mechanics, musculature, tooth function, etc.—is

therefore within Wroe et al.'s grasp, but information about coat color patterns (for example) is not. Zachos and Sprinkle can predict likely echinoderm physiologies by modeling developmental systems shared by all Echinodermata, but they cannot predict the contingent ecological roles of particular echinoderms without additional fossil evidence. The range of inference from one hierarchy to another is always limited by the level at which information is found and so there is always some room for pessimism in hierarchical inference.

Other ostensible examples of paleontological success also show the limits of optimism in hierarchical inference. Daeschler et al. wagered that something like *Tiktaalik* awaited discovery in Northern Canada, but couldn't anticipate features of the animal's physiology such as its forelimb structure (Laurin 2006). Their ability to predict *Tiktaalik*'s physiological features was limited by the hierarchical information supporting their wager: *Tiktaalik* should occupy a particular spot between two grades in the tetrapod phylogeny, but that taxonomic spot implied nothing in particular about forelimb physiology. Similar inferential limitations characterized the discoveries of stem-whales and stem-turtles. In the first case, paleontologists were surprised by the artiodactyl-like limb structure of "walking whales"; in the second case, paleontologists did not anticipate that the earliest turtle shells included a lower plastron and not an upper carapace. These physiological features were not predictable from taxonomic information even though the taxonomic information was sufficient to predict the fossils' geographic locations. In all these cases, as in Currie's given cases, paleontologists were willing to place only a limited range of bets.

Fortunately, the range of wagers that paleontologists are willing to make increases with greater access to the fossil record. The discoveries of stem-tetrapods, stem-whales, and stem-turtles increased the range of inferences that paleontologists can make between hierarchies. We now know that the taxonomic range of turtles in the clade Testudines may imply a wider range of physiological information or that ecological information associated with shallow-water waders correlates with early tetrapod relatives. New fossils permit greater success in reconstructing life's history because those fossils open inferential bridges between biological hierarchies.

Unfortunately, paleontologists are often unable to know where to construct those inferential bridges. Paleontologists study extinct life, after all, and extinction 'erases' information from biological hierarchies (Marshall 2017). The taxonomic hierarchy no longer includes stem-marsupials, stem-echinoderms, stem-tetrapods, stem-whales, or stem-turtles, and various particular facts about those animals' physiologies and ecological roles have therefore disappeared from those hierarchies as well. Those facts would anchor points of connection between hierarchies and so the extinction of the relevant groups diminishes our inferential abilities. Without the relevant fossils, our understanding of extinct forms of life follows only from existing ranges of connection between hierarchies—and those connections are often insufficient to understand life's past diversity.

These limitations do inform Currie's view. He endorses a more tempered version of optimism later in the book: "For any (important) past good, g, I'd be willing to bet that historical science will learn g—unless g has particular features that make its recovery unlikely" (2018, 283). We can be optimistic where connections between hierarchies allow it, but the range of those connections establishes bounds for optimism. In this framing, the basis for Currie's optimism is paleontologists' aptitude in using fossils to establish new or broader connections between biological hierarchies.

Understood in the sense given above, the wager that paleontologists will tend to be successful in reconstructing past life is ultimately underwritten by optimism about future fossil discoveries. If paleontological investigations tend to be successful because paleontologists are good at establishing new connections between hierarchies, and if the range of connections be-

tween hierarchies depends on contingent discoveries of fossils (and other traces), then success in paleontology depends on the discovery of new fossils. Currie's argument for optimism in paleontology therefore depends logically on his optimism about fossil discoveries.

Currie does endorse this second-order optimism about optimism: pessimists tend to "understate the total evidence ultimately available" (278). This may be true in general, but particular circumstances may demand a different take. In these particular cases—wagers about specific fossil finds or paleontological research projects—Currie's optimism may be paradoxically consistent with second-order pessimism. To understand why, I offer one final example.

4   Conclusion: Where Should We Place Our Next Bet?

The taxonomic grade Pelycosauria includes a variety of reptile-like mammal relatives such *Dimetrodon*. Often confused for a dinosaur, *Dimetrodon* is perhaps most notable for a series of elongated neural spines that create an arch-shaped pattern along the animal's vertebral column. These spines may have supported a "sail" of soft tissue. "Sails" are relatively common among pelycosaurs, appearing in other genera such as *Ctenospondylus*, *Edaphosaurus*, *Ianthasaurus*, *Secodontosaurus*, and *Sphecanodon* (Benton 2014, 118–143).

Although common among these stem-mammals, sails are relatively rare in evolutionary history and almost entirely unknown among extant animals. Other animals with neural spine sails include the amphibian *Platyhystrix*, the dinosaurs *Amargasaurus*, *Ouranosaurus*, and *Spinosaurus*, and, debatably, a handful of extant species such as the crested chameleon and buffalo. The latter two cases are debatable because their neural spines differ from those found in other sail-backs both in relative length and overall structure. In fact, structure is a general problem in the study of neural spine sails: the forms taken by elongated neural spines are widely variable. This physiological variability, when combined with the taxonomic disparity between sail-backed animals, confounds paleontologists' efforts to understand the form or function of neural spine sails (Benton 2014).

By the account given above, the ongoing problem is that paleontologists cannot establish connections between biological hierarchies useful for studying sail-backed animals. The diverse sail-backs have little in common ecologically; the broad physiological similarities between them do not imply any particular facts about ecology or taxonomy; the taxonomic variety listed above defies any more specific inference than those we can draw about all tetrapods. I have suggested that solving this puzzle would require expanding the range of inferences that paleontologists can draw between biological hierarchies through the discovery of a paleontological Rosetta Stone. This may come in the form of a particularly detailed fossil that includes soft tissue preservation or a trace that authoritatively reveals some sail-backed animal's behavior.

Should we wager that paleontologists might someday discover one of these potential fossils? Note that this would not be a wager about paleontologists' methodologies (cf. Turner 2016): it would instead be a wager about the likelihood that the fossil record includes some particular trace. The former kind of wager seems more likely to pay off: as noted above, paleontologists commonly develop new (or borrowed) methodological tools. But if we're less likely to take the second wager than we are to take the first, this would suggest that we can be both first-order optimists (optimists about research outcomes, i.e., the sort of optimism for which Currie argues) and second-order pessimists (i.e., pessimists about the fossil discoveries that enable successful research outcomes).

If first-order optimism depends on second-order optimism, as I have suggested above, this result is paradoxical. The remaining question, then, is whether or not I have fairly characterized

Currie's view. Whatever the case about fossils, I am optimistic about the resolution of that question.

Acknowledgments

Literature cited

Benton, M. 2014. *Vertebrate Palaeontology*. Fourth edition. New York, NY: Wiley-Blackwell.

Currie, A. 2018. *Rock, Bone, and Ruin: An Optimist's Guide to the Historical Sciences*. Cambridge, MA: The MIT Press.

Daeschler, E. B., N. H. Shubin, and F. A. Jenkins Jr. 2006. "A Devonian Tetrapod-Like Fish and the Evolution of the Tetrapod Body Plan." *Nature* 440 (7085): 757–763. doi:10.1038/nature04639.

Eldredge, N. 1991. *Macroevolutionary Dynamics*. New York, NY: McGraw-Hill.

Laurin, M. 2006. "Scanty Evidence and Changing Opinions about Evolving Appendages." *Zoologica Scripta* 35 (6): 667–668. doi:10.1111/j.1463-6409.2006.00256.x

Li, C., X. C. Wu, O. Rieppel, L. T. Wang, and L. J. Zhao. 2008. "An Ancestral Turtle From the Late Triassic of Southwestern China." *Nature* 456 (7221): 497–501. doi:10.1038/nature07533.

Madar, S.I., and J. G. M. Thewissen. 1994. "Vertebral Morphology of Ambulocetus, an Eocene Cetacean from the Kuldana Formation (Pakistan)." *Journal of Vertebrate Paleontology* 14 (3): 77–104.

Marshall, C. R. 2017. "Five Palaeobiological Laws Needed to Understand the Evolution of the Living Biota." *Nature Ecology & Evolution* 1 (6): 1–6. doi:10.1038/s41559-017-0165.

Turner, D. 2016. "A Second Look at the Color of Dinosaurs." *Studies in History and Philosophy of Science Part A* 55: 60–68. doi:10.1016/j.shpsa.2015.08.012.

Wroe, S., C. McHenry, and J. Thomason. 2005. "Bite Club: Comparative Bite Force in Big Biting Mammals and the Prediction of Predatory Behavior in Fossil Taxa." *Proceedings of the Royal Society B, Biological Sciences* 272: 619–625. doi:10.1098/rspb.2004.2986.

Wylie, C. D. 2015. "'The Artist's Piece Is Already in the Stone': Constructing Creativity in Paleontology Laboratories." *Social Studies of Science* 45 (1): 31–55. doi:10.1177/0306312714549794.

Zachos, L., and J. Sprinkle. 2011. "Computational Model of Growth and Development in Paleozoic Echinoids." In *Computational Paleontology*, edited by T. Elewa, 75–94. Heidelberg: Springer International Publishing.