

# Fossils, Modality & Central Subjects in Palaeobiological Reconstruction

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Paleobiology is not only a science of the deep past: it is a science of deep possibility. Drawing on recent speculative reconstructions of *Spinosaurus aegyptiacus*, I sketch a new account of paleobiological reconstruction. Fossils, as opposed to testing causal hypotheses, are used to characterise and evidence the ‘central subjects’ of paleobiological reconstruction, in this instance, particular dinosaur taxa. These central subjects are then situated in various ‘profiles’, representational tools which isolate particular traits across several dimensions in order to apply comparative methods which generate and test often modal hypotheses. I suggest this represents a particular phenomena-driven mode of exploring possibility, one with distinct advantages over approaches more common in theoretical evolutionary biology.

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## Keywords

historical science • evidence • traces • possibility

## 1 Introduction

I’m going to say something new about reconstruction in vertebrate paleobiology, and about the role fossils play within it. To front-load the jargon: I’ll argue that paleobiological reconstruction proceeds via situating a central subject in a variety of modal spaces, or ‘profiles’ as I’ll call them, and that fossils primarily evidence and characterize central subjects. That’s a mouthful right from the outset. Although all will be explained in due course, I hope it helpful at this point to contrast my account with what I’ll call the *traditional view*.


On the traditional view, fossils serve as primary evidence for testing hypotheses about the actual palaeobiological past<sup>1</sup>. The hypothesis “Tyrannosaurs were feathered” is evidenced via fossils causally downstream of individual organisms hailing from that lineage—fossils that are

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1. This is a version of what Currie has called ‘trace-based reasoning’ (Currie 2019a; Currie and Killin 2019). Views most aligned with what I’m calling ‘traditional’ include Cleland (2001, 2002), Tucker (2011), Turner (2005, 2007).

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reasonably interpreted as feathered—and weakened by otherwise similar specimens without evidence of feathers. On this view, fossils and other ‘trace’ evidence, combined with relevant background theories, can, under the right conditions, evidence hypotheses concerning the actual past. Here, paleobiology is (1) primarily interested in uncovering the actual past, (2) uses fossils to test hypotheses concerning that actual past and further, (3) reconstruction is mediated by background theories that explain fossil formation.

On the view I’ll introduce, (1) paleobiology is interested in the development and application of *profiles*, that is, highly particular spaces of biological possibility—the actual is at the least a complementary, and sometimes a secondary, goal—(2) fossils primarily function to evidence and characterize central subjects (typically extinct lineages), and (3) reconstruction occurs when that central subject is situated across various profiles to generate a coherent scenario or narrative. In this instance, arguing that *Tyrannosaurs were feathered* will involve using fossils to characterize a particular phenomena—the *Tyrannosaur* lineage, their morphology, etc.—which are then situated within their phylogenetic context (one profile), compared to other feathered vertebrates (another profile), considered via various biomechanical models (yet another set of profiles) and so on. Moreover, in so doing, our conception of those profiles—what is possible for feathered vertebrates to be like, for instance—themselves is influenced and changed.

This perspective on paleobiological reconstruction has some important consequences. First, it shows that, even in reconstructions of charismatic vertebrates, paleobiology is just as, if not more, concerned with what is possible as with what was actual. This matters for understanding the purpose, value and scope of paleobiological work. Second, it emphasizes the role of integration and coherence in strategies of reconstruction<sup>2</sup>. Third, it provides an interesting counter-perspective to other sciences concerned with possibility, namely, various forms of theoretical models in biology and beyond. Where the constraints on possibility in those practices are more-or-less provided by theory alone, in paleobiology theory has an intimate, iterative relationship with specimens relating to an actual history. In virtue of this, paleobiologists have resources for claiming they are studying *relevant* modal spaces which these other scientists lack.

Recent papers on the epistemic nature of fossils have focused on fossils *as* data and how scientists interact with them as such (Bokulich 2021; Leonelli 2018; Currie 2021; Wylie 2019, 2024; Watkins 2024). Such work emphasizes the significant journeys undertaken by ancient biological phenomena from death, decomposition, preservation and discovery, through extraction, preparation and analysis. Here, I’m interested in the evidential use of fossil data. Where the traditional view takes them as primary evidence for explanatory hypotheses, I’ll show they also function in phenomena-characterization. As such, I think analyses of fossils-as-data and fossils-as-evidence-for-phenomena are complementary.

I’ll make my argument in reference to an illustrative case study: recent work on the functional morphology and ecology of *Spinosaurus aegyptiacus*, which we’ll turn to in section two. With the relevant details in hand, in section three I’ll abstractly characterise the notion of ‘profiles’ and show how these operate in reconstruction. In section four, I’ll talk about the role of fossils, drawing on the explanatory notion of ‘central subjects’ and providing an additional epistemic role for them. In section five I’ll wrap up, noting in particular the kind of specimen-grounded explorations of possibility so characteristic of reconstruction in paleobiology. Before starting, a few caveats.

First, there is no one philosophical account of method in the historical sciences in general, nor of paleobiology in particular (Currie 2018, chapter 6). Although this paper is framed as being at loggerheads with what I’ve called the traditional view, I hope it clear that there are cases where that view’s relatively simple inductive logic captures what is going on perfectly well, while

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2. For emphasis on coherence in historical reconstruction see Kosso (1993), Currie (2017).

other circumstances require the more complex mechanics I introduce. For the purposes of this paper, the traditional view is a useful foil for getting a sense of what makes my account original, but we're not playing an all-or-nothing, winner-takes-all kind of philosophical game. So, the traditional view taken as a complete account of reconstruction should be rejected in favour of pluralism. Quite often, I suspect, the two approaches are complementary.

Second, as should be familiar, I'll be making an apparently more-general claim about how palaeobiological reconstruction—sometimes—proceeds, on the basis of a single case study. I've not the space here to rehearse the various defences one might have of this approach, so instead happily admit that my analysis could turn out to be due to some quirk of *Spinosaurus* research rather than a pattern (although I doubt it)<sup>3</sup>.

Third, I don't in any way mean to imply that work on *Spinosaurus* research represents all that vertebrate paleobiologists might be interested in: developing profiles and reconstructing extinct lineages sits along-side more data-intensive work on macro-evolutionary patterns and theory, for instance—although this is typically carried out using invertebrate fossils (Erwin 2024). Just as we shouldn't expect a single philosophical analysis to capture the epistemic structure of the historical sciences generally, so also we shouldn't expect study of past life to fall into lockstep with analyses of functional morphology in vertebrate paleobiology.

Fourth, there are at least two areas where modality's crucial place in paleobiology is well-recognised. Longstanding discussions of macroevolutionary contingency are interested in the robustness or otherwise of outcomes at broad biological scales, and a rich scientific and philosophical literature explores these questions (e.g., Turner and Havstad 2019). I won't say anything substantive about that literature in this paper, but it is worth noting that my emphasis on the role of fossils potentially advances our epistemic understanding of how fossils ground those explorations. Further, the centrality of model-based reasoning is well-recognised by philosophers interested in the historical sciences (Turner 2009; Wylie 2017; Bokulich and Oreskes 2017; Currie forthcoming). The big news here isn't that models and modality matter, but how modal knowledge is generated, and the role of fossils in that practice. Indeed, one might think that the reconstruction of dinosaurs and other charismatic fauna is one place where focus on the actual should be expected: after all, we want to know how these fascinating animals in fact went about their lives. So, showing that even here modal knowledge is central is a potentially powerful way of emphasizing possibility in the historical science more generally<sup>4</sup>.

Having said this, fifth, I'm purposefully cagey about whether the claims I make about paleobiological reconstruction might be so extended. I bet they can be, and in interesting ways, but this paper has enough to be getting on with. So, in that spirit, let's be getting on with things.

## 2 *Spinosaurus aegyptiacus*

Despite the mystique surrounding vertebrates leaving the water and colonizing terrestrial environments, secondarily aquatic vertebrates are a remarkably diverse and common paraphyletic group (Gutarra and Rahman 2022). Given this diversity, we might wonder: Do any dinosaurs belong among the seals, platypus and ichthyosaurs? Although aquatic environments were a commonly proposed solution to the apparent overbearing size of Sauropods in the first half of the twentieth century, only in the last few years have contemporary paleontologists attempted to seriously identify a secondarily aquatic dinosaur. And the candidate is surprising: a huge, bipedal theropod.

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3. For discussion of case-study based methods in the philosophy of science, see Currie (2015b).

4. Many thanks to an anonymous referee for suggesting this approach.

The Spinosaurids are a diverse and well-dispersed family of theropod dinosaurs hailing from the first-half of the Cretaceous (Berlin 2010). Our subject—*Spinosaurus aegyptiacus*—is the longest theropod dinosaur as yet discovered, reaching lengths of around 14 meters, and weighing 7.4 ton in a recent reconstruction (Sereno et al. 2021)<sup>5</sup>. Although the lineage was first described in 1915 (with its piscivorous traits already noted; Stromer 1915), the holotype's being destroyed in the Second World War, and a lack of new finds, led to not much happening in *Spinosaurus* science throughout the twentieth century. Although photos eventually emerged of the holotype, I suspect that without the original specimen to return to, paleontologists were less willing to speculate about the lineage's form and function. (I'll return to this below.)

That period of relative silence was shattered in 2014 when Ibrahim et al. (2014) published an analysis of a remarkably complete specimen, establishing it as a neotype. They emphasized various aquatic adaptations: non-pneumatized bones, a long-neck and thin-jawed morphology often associated with fish-eating, nostrils placed midway up the skull reminiscent of the raised nostrils of crocodylians and hippopotamus, shorter hindlimbs and reduced pelvis relative to other theropods, and so forth. And indeed, there are important similarities between *Spinosaurus* morphology and aquatic or semi-aquatic fish eaters (e.g., Vullo, Allain and Cavin 2016).

So, it seems plausible that *Spinosaurus* was somewhat adapted to an aquatic lifestyle, be it that of a semi-aquatic carnivore or a land-based critter haunting the margins of waterways. But should we be imagining something like a brown bear (the latter) or something like a seal (the former)? That is, is *Spinosaurus* a largely terrestrial animal with some aquatic adaptations, or a largely (secondarily) aquatic animal that occasionally ventured onto land (or something in between)?

I've argued that historical science often progresses on the back of highly speculative—yet productive—hypotheses, and *Spinosaurus* research since 2014 certainly fits the bill. In response to Ibrahim et al.'s paper, paleontologists have questioned the find's taphonomic and stratigraphic properties, built various models probing the lineage's buoyancy, terrestrial gait, and hunting capacities, and doubted the veracity of Ibrahim et al.'s fossil. And Ibrahim et al. responded with their own studies, incorporating digital techniques, as we'll see, and further taphonomic evidence (for instance, Beevor et al. 2021). I'm not interested here in coming down one way or another on *Spinosaurus* (see Hone and Holtz 2021; Brusatte 2021 for summaries)—that's surely above my paygrade—but in the remainder of the section I'll highlight a few studies to draw on downstream.

In response to Ibrahim et al.'s appeal to the buoyancy properties of *Spinosaurus* in the 2014 paper, Don Henderson constructed three dimensional models of *Spinosaurus* and a set of other lineages (Henderson 2018): closely related *Spinosaurids* and other theropods (including *T. rex* and *Allosaurus*). These models represent information about density, simulated lungs and air-sacks, and thus explore various aquatic properties. For our purposes, Henderson makes two main points against the pursuit-predator hypothesis. First, against Ibrahim et al.'s emphasis on *Spinosaurus*'s capacity to float, he points out that although in their model *Spinosaurus* could float, so also could *T. rex*—an animal that no one thinks is semi-aquatic. The thought seems to be that pointing at the buoyancy properties of *Spinosaurus* in support of their being semi-aquatic is only relevant if these features draw them *apart* from their non-aquatic relatives. However, as their modelling shows, “there is nothing exceptional about a floating *Spinosaurus*” (Henderson 2018, abstract). Potentially more damning, Henderson also argued that the *Spinosaurus* could not sink: its bird-like air-sacks and pneumatized limbs were insufficiently dense. Penguins have non-pneumatized skeletons to achieve aquatic sink. There is a question-mark here: I've not found a conclusive statement

5. There is a lack of clarity regarding whether there are multiple species within the genus *Spinosaurus*, but I'll stick to the genus name rather than the species name.

vis-à-vis the pneumatization of *Spinosaurus*<sup>6</sup>. If their skeletons are not significantly pneumatized, I would think that quite telling of an aquatic lifestyle (maybe they're not seals but penguins). Insofar as the lineage's pneumatization or otherwise is up for grabs, however, there's not much to say in this context.

Henderson's paper is a single example of the kind of challenges Ibrahim et al.'s hypothesis has faced, but is sufficient to capture their flavour. As I'll expand on in the next section, Henderson isolated a set of *Spinosaurus* properties (their capacity to float, their capacity to dive), put these in a comparative context, and examined the range of capacities under biologically relevant constraints. Ibrahim et al.'s original analysis, and their responses, adopt a similar strategy.

In light of various objections, in 2020 Ibrahim et al. doubled-down on the aquatic-pursuit hypothesis (see also Gimsa and Gimsa 2021). In addition to various simulation studies similar to Henderson's, they also undertook a simple robotics experiment<sup>7</sup>. Plastic sheets were cut to proportionally resemble the tails of various reptiles: *T. rex*, newts, and *Spinosaurus*. These were submerged in an aquatic flume and waggled left-to-right or up-and-down by a robotic arm, thus generating aquatic propulsion. The results, they claim, speak to the *Spinosaurus*'s aquatic prowess: "Overall, the vertically expanded tail shape of *Spinosaurus* imparts a substantial positive benefit to aquatic propulsion relative to the long and narrow tails of terrestrial theropods, supporting the inference that *Spinosaurus* used tail-propelled swimming" (Ibrahim et al. 2020, 69). This suggests to some extent that *Spinosaurus* tails were well-adapted to fast swimming.

I've not attempted a complete account of recent work on *Spinosaurus* (for one thing I've not touched upon the various hypotheses concerning its large dorsal sail and how that might relate to its swimming capacities, see Gimsa, Sleigh and Gimsa 2016). Rather, I've aimed for a kind of taster, which underwrites the account of reconstruction I'll now turn to.

### 3 Profiles & Reconstruction

On what I've called the traditional view, fossils act as primary evidence for testing between explanatory hypotheses concerning the deep past. In light of section 2, that view, on the face of it, cannot accommodate cases like *Spinosaurus* reconstruction. Rather than fossils being used as evidence to test hypotheses, particular inferred information about *Spinosaurus*—its functional morphology, phylogenetic setting, etc.—is set in various comparative contexts: with other piscivores, other secondarily-aquatic vertebrates, other reptiles, and so on, and various pseudo-experimental practices, from simulations to concrete models, are used to test hypotheses within those contexts. It may be that a determined defender of that view wants to insist that ultimately causal hypotheses concerning fossils are what are being tested (the third part of the traditional view, above), but in this section, I'll take a different route: characterising this more indirect route to reconstruction using what I'll call *profiles* (Currie 2021b; see Lauder 2022 for similar ideas).

In each of the studies sketched above, some set of putative *Spinosaurus* properties are isolated and represented so that those properties may be compared with other critters or made amenable to various tests. In their 2014 paper, Ibrahim et al. isolated various features of *Spinosaurus* morphology (nostril position, for instance), which indicated aquatic lifestyle via plausible function aligned with relevant analogies (hippos, for instance). Henderson isolated morphological features relevant for *Spinosaurus*' buoyancy, comparing those properties with other large dinosaurs. In

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6. It seems that it is agreed that *Spinosaurus* is somewhat pneumatized, as Hone and Holtz put it "The exact extent of the pneumaticity of *Spinosaurus* is not known, but the cervicals and dorsals do at least show pneumatopores" (2021, 15)

7. For discussion of the use of robotics in paleobiology and functional morphology see Tamborini (2020, 2021).

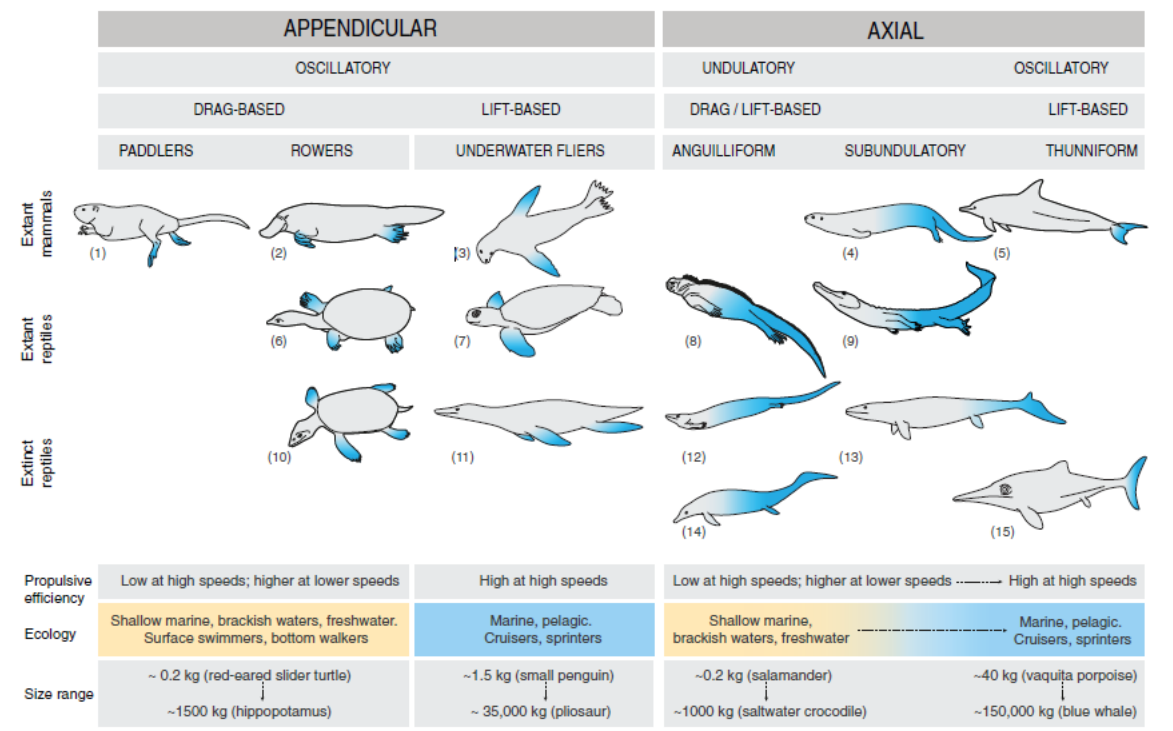


Figure 1: Example of a 'profile' from Gutarra and Rahman (2022: figure 6), CC:BY.

2020, Ibrahim et al. isolated tail morphology vis-à-vis propulsive capacity, comparing this with extinct and living reptiles. Indeed, analysis of *Spinosaurus* seems to involve continual isolation of various properties in order to set them into a comparative context: sometimes the lineage is conceived of as a secondarily-aquatic vertebrate, sometimes a theropod, sometimes an aquatic-pursuit predator. In reconstructing *Spinosaurus*, paleontologists take what knowledge of the phenomenon they have, and situate it across various 'profiles'.

A *profile* is an abstract space characterized by a set of biologically relevant properties, into which various exemplars are situated in order to generate and test hypotheses. These are often represented as dimensions. For instance, a *morphospace* such as Raup's (1966) classic shell space consists of a set of geometrically-derived dimensions representing (in Raup's case) shell growth. Into this theoretical space the actual distribution of known actual shells can be placed. For another instance, a *cladistic phylogeny* uses morphological or molecular characters to align lineages in terms of sister-clades and outgroups. This enables inferences concerning character-evolution, the timing and order of evolutionary change, and so on. Some profiles are highly specific. Ibrahim et al.'s robotic tails, for instance, classify various reptiles in terms of tail shape, and experimentally link tail-shape to potential propulsion. Profiles often mix various biological categories. Gutarra and Rahman (2021), for instance, combine a paraphyletic group (secondarily-aquatic vertebrates) with a set of functional morphological characteristics tracking swimming 'gait' (see figure 1). This enables the exploration of the actual distribution, and the generation of new hypotheses. Why, for instance, are there no reptilian paddlers? Why are turtles so well represented across appendicular swimming styles?

'Profiles', then, are abstract spaces composed of biological properties into which particular lineages holding the relevant properties are situated, both to evidence the profile and to generate and test hypotheses concerning those lineages. Crucially for my analysis, profiles often generate, contain, or motivate tests of, modal information. Although I'll expand on this in section 5, it

is worth briefly considering a fairly deflationary account of the epistemic roles of profiles to emphasize their diversity.

In a recent paper, Novick et al. characterise what they call *Kon-Tiki Experiments* (2020). At base, Kon-Tiki experiments are in the business of experimentally establishing whether some capacity required by a past hypothesis is *possibly held* by the relevant target. The hypothesis that the Pacific was settled from South America via drift-voyaging is presaged on the idea that the craft available at the time were able to drift-voyage from South America to the Pacific. By constructing as relevantly similar a craft as possible, and successfully making the voyage, Thor Heyerdahl established that capacity. Tellingly, however, this doesn't establish the actuality of such voyages—indeed, later Kon-Tiki-style experiments take some responsibility for showing how sophisticated navigational and shipbuilding technologies enabled purposeful settlement from south-east Asia. A Kon-Tiki experiment, then, constructs a reasonable simulacrum of a past object to experimentally probe whether said past object was capable of behaving in ways posited by the relevant hypotheses. Should we think of the use of profiles in Kon-Tiki terms alone? No.

First, profiles are often significantly more abstract and idealized than Kon-Tiki experiments. Consider Ibrahim et al.'s tails. Although both involve the construction of a concrete object thought to be epistemically relevant, Ibrahim et al. didn't aim for realism, rather they were attempting to isolate and explore the relevant properties of tail-like geometric shapes. As Gutarra and Rahman point out:

Some limitations of this study are the simplicity of the robotic structure design (i.e., a flat plastic tail profile mounted on an undulating rack) and the fact that motion, although set to an amplitude and speed informed by living undulatory swimmers (salamanders of the genus *Amblystoma* and the American alligator) did not account for specific anatomical constraints (i.e., vertebral motion ranges, flexibility, muscle configuration). (Gutarra and Rahman 2021, 20)

Second, Ibrahim et al. were not directly testing whether *Spinosaurus* tails could enable the critter to engage in fast underwater pursuit, rather they were placing it in a comparative context in order to provide evidence that the tail's design afforded better thrust than relevant competitors. Insofar as this established a capacity, it did so far more indirectly than Heyerdahl's voyages.

Third, consider Henderson's argument. By showing that some non-swimming theropods—including *T. rex*—have similar buoyancy properties as *Spinosaurus*, he argued that those properties shouldn't be considered evidence in favour of *Spinosaurus* being a swimmer. Instead of the test establishing the capacities of some past target towards establishing possibility if not actuality, Henderson argues that the property at hand does not distinguish the target from relevant comparators, and so is evidentially inert. This has a different epistemic structure than a Kon-Tiki experiment.

Many of the profiles discussed here include apparently adaptationist elements: for one instance, Ibrahim et al. link the relative optimality of *Spinosaurus* tail design for aquatic thrust to the actual role it played; for another instance, the connection between the elongated snout and piscivory isn't merely based on similarity, but the presumed adaptiveness of that design for fish-hunting. As Martin Rudwick has put it, such attributions of function rely not only on mere analogy between living animals and fossil taxa, but “depend fundamentally on applying a criterion of *mechanical fitness*” (Rudwick 1964, 33, italics in original), that is, our engineering knowledge of how various structures might be suited to various tasks. I think there is work to be done understanding how exactly adaptationist ideas play into paleobiological reconstruction (in addition to Rudwick, see Turner 2000; Currie 2015a), but haven't space here to develop anything substantive. Briefly, it is worth noting three things. First, the role of optimality is often somewhat

ambiguous and backgrounded in paleobiological reconstruction, perhaps sometimes egregiously and sometimes usefully. Second, not all profiles rely on such principles: it depends crucially on the biological properties that are isolated (phylogenies and some morphospaces come to mind). Third, although the particular tests a profile affords might depend upon criteria of mechanical fitness, such assumptions are far from untestable, in particular, the validity of results typically turn on how they come together in a picture of the organism as situated in its evolutionary history and environment. In the next section, I'll argue that central subjects characterized by fossils and other traces afford this. As such, the account provided here might provide a richer story about how adaptationist hypotheses and thinking are tested and integrated into paleobiological reconstruction.

So, different profiles are built from a wide variety of biological properties, and are put to a wide variety of epistemic uses. And this is the point. Historical reconstruction requires flexibility, partly because of the oft-impooverished epistemic situation we face, and partly because of the complexity of past targets. Profiles afford this flexibility.

Hopefully you now have a grip on one half of the view of historical reconstruction I am proffering: instead of testing hypotheses with fossils, paleobiologists often test hypotheses by situating the relevant targets into various profiles. These profiles offer a modal and comparative context that affords—in the good case—rich reconstructions. However, you might have at least two, linked worries at this stage. Worry the first: Why should we think these profiles, varied and abstract as they are, are *biologically relevant*? Worry the second: How could debates such as that surrounding *Spinosaurus* be unified, as varied and abstract as they are? To answer these two worries arising from the abstraction and variation of profiles, we need to fill in the second part of the account, turning to the role of fossils in characterizing central subjects.

## 4 Fossils & Central Subjects

David Hull's classic discussions of *central subjects* aim to address two questions concerning narrative explanations (Hull 1975; Ereshefsky and Turner 2020). First, how do (if they do) narratives suffice *as explanations*? That is, how do they take us from a mere description of a set of events to an explanation of those events? Second, how are (if they are) narratives *unified*? That is, what accommodates the coherence of such explanations? Hull's contrast was covering-law models which had dominated discussion of explanation. By such accounts, scientific explanation is explanatory in virtue of tracking a deductive inferential structure: explanations were considered sets of sentences wherein the explanans acted like premises in an argument from which the explananda logically followed. They were unified in virtue of the general laws appealed to: covering laws which also provided the necessary modal oomph to get from a 'what' to a 'why'. But narratives neither involve deduction nor laws, yet seem explanatory.

*A central subject* can be understood as a particular historical individual that a narrative explanation is about. "The role of the central subject is to form the main strand around which the historical narrative is woven .... Central subjects afford the basic unity and continuity of the historical narrative" (Hull 1975, 255). If I am to tell the history of, say, the *Emu Wars*, I don't begin by picking out a general phenomenon, say, types of wars. I instead pick out a particular set of events in Australia in the early twentieth century (Johnson 2006). I might point to the rapid growth of agriculture in Australia, coupled with a decrease in predation, leading to boom-bust cycles across emu populations. I might then point to the impact those population changes had on Australian agricultural production, coupled with various idiosyncrasies of Australian politics leading to the Australian army being deployed on an ill-fated emu cull. I might then explain the rather blatant failures of the Australian army in the 'war' as being due to a combination of the



natural emu tendency to scatter with the unsuited machine-gun-based tactics the Australian army inherited from the First World War. The explanation is a what rather than a why because of how the causal events posited lead to the relevant outcomes, and the various aspects are unified because they pick out a token, *de re*, historical trajectory: the emu war itself.

So, the notion of a central subject has been usefully deployed to get a handle on the explanatory features of narratives. Here, I make use of them in a different epistemic context. In the last section I raised worries about the unity and relevance of profiles. Why should we think that the various isolated profiles and modal spaces paleobiologists employ are biologically relevant, and what makes their debates hang together? We can employ central subjects analogously to the work they do for narrative explanations: the central subject plays a double role in making sense of how the various elements hang together and ensuring relevance.

In the case at hand, the central subject is an historical individual: the *Spinosaurus* lineage. The various profiles which isolate properties and examine them are relevant because they are putative *Spinosaurus* properties. The various studies come together—are unified—by the historical individual, that is, the *Spinosaurus*. This is what links Gutarra and Rahman's category 'secondarily aquatic vertebrate', Henderson's profile of the buoyancy properties of various dinosaurs, and Ibrahim et al.'s study of tail propulsion: each of those target properties are putatively held by *Spinosaurus*. What makes the studies plausibly biologically relevant is that they are developed to directly test questions arising from *Spinosaurus*' history. To paraphrase Hull, the central subject forms the main strand around which the investigation proceeds. So, to fossils.

The original *Spinosaurus* holotype, described in the early twentieth century, was destroyed in the Second World War. Although fairly detailed photos and diagrams survived (allowing relatively accurate reconstructions; Smith et al. 2016), it wasn't until Ibrahim et al.'s discovery of a remarkably complete specimen in 2009 that productive investigation into that lineage really took off. Part of the explanation of 70 years of relative calm vis-à-vis *Spinosaurus* speculation is, I think, the lack of fossils. In vertebrate paleontology, actual fossil remains act as a kind of epistemic bedrock, an ultimate arbiter, of epistemic activity. Fossils act as *investigative anchors*, shaping speculation, testing and modal exploration. Prior to the discovery of the neotype, there wasn't something for paleobiologists to, as it were, *go back to*, in their disputes. As Wylie has put it, "regardless of whether data processing is digital or physical, researchers hold physical fossils as the bearers of 'truth'" (Wylie 2021, 124).

I think the right way of characterizing the priority that fossils appear to take in paleontological research isn't always as primary evidence that tests hypotheses, but as the main resource for *characterizing phenomena*, which is to say, inferring the features of the central subjects around which the rest of the investigation is structured. I don't by this mean to suggest that fossils don't test hypotheses. Indeed, characterizing phenomena *is* a hypothesis-testing pursuit. However, it is interested in accounting for a *de re* process in the record that then requires explanation. In this issue, Doug Erwin distinguishes 'descriptive' paleontology from explanatory, analytic and integrative paleontology. The former, I take it, is largely in the business of characterizing the patterns which then become the fodder for the latter three's investigations. Max Dresow relies on a similar distinction when he argues that "a major 'driver' of explanation in geohistory is non-explanatory work—work that is undertaken to increase the descriptive understanding of a phenomenon, not to test a particular explanatory claim" (2021, 1047). Dresow's claim regarding the importance of descriptive work in macroevolutionary studies dovetails nicely with the idea that in vertebrate paleontology fossils are central for identifying and characterizing central subjects.

How should we characterise this distinction between 'descriptive' and 'explanatory' work in paleobiology, when both clearly involve hypothesis-testing? Here's my provisional answer. We can understand *descriptive* hypotheses as primarily explaining traces—fossils, say—in terms

of their past causes, especially theories of trace-formation. Ibrahim et al. argue that their *Spinosaurus* reconstruction comes from a single individual by pointing to various features of the incomplete find. For instance, if the fossils all appear to be from an organism of the same age, this suggests they're from the same organism: "should histological details suggest that all five elements represent the same ontogenetic stage, then the remains are more likely to represent one individual than multiple individuals" (Ibrahim et al. 2020, 71). Thus, osteological similarities signal a common source. Similar could be said of attempts to characterize patterns and trends in the fossil record: whether they are best explained by biological processes or, say, by biases in preservation. *Explanatory* hypotheses target not the specimens themselves, but rather past phenomena descriptive hypotheses have characterized. For instance, Ibrahim et al.'s *Spinosaurus* has raised nostrils, and they posit that these function to aid breathing in semi-submerged contexts à la hippopotamus. Thus, *descriptive* hypotheses explain features of traces by characterizing past entities, events and processes, while *explanatory* hypotheses explain features of those past entities, events and processes. I suspect this account might be infelicitous in some contexts, but captures something like what Erwin, Dresow and I are getting at.

Notice that fossils are both central subjects and evidence for them. Caitlin Wylie (2024) describes a fossil preparator seeking to draw together various scattered parts in repairing the skull of an extinct horse-like mammal. In her discussion, we might take the fossil itself—the specimen—as the central subject around which the data-journey she describes is woven. But so also can fossils evidence central subjects: they are a major resource for the identification and characterization of extinct animals. Aja Watkins (2024) asks whether we should include human-independent fossil processes in addition to discovery, extraction and preparation, as part of a fossil's 'data journey' (Leonelli and Tempini 2020). Taking fossils as central subjects suggests at least one context-dependent answer to this question. Sometimes paleontologists are interested in understanding the life of a fossil in particular, and in these instances the fossil is the central subject, it is the phenomenon we seek to understand. For instance, when Ibrahim et al. (2020) attempt to persuade us that the assemblage of fossils they present are from the same individual, they are telling a story about the individual fate of that fossil post-death. But they are telling that story in aid of a further epistemic activity: characterizing the *Spinosaurus* lineage as a central subject. What counts as data and what as phenomena, here, turns on the particular details of that discussion, and indeed scientists often switch between these as dictated by the needs of their epistemic activities. This is no problem for our analysis, I think, but rather the kind of flexible dynamism we should expect from opportunistic science.

In this paper's first paragraph I said: *paleobiological reconstruction proceeds via situating a central subject in a variety of modal spaces, or 'profiles' as I'll call them, and ... fossils primarily evidence and characterize central subjects*. Hopefully what I mean by this is now clear. I take it this is a different, less-direct and more complex view of how reconstruction sometimes proceeds in the historical sciences. An open question here concerns the division of labour between profile-oriented strategies and the simpler logic associated with the 'traditional view', which is to say, When should paleobiologists test explanatory hypotheses with fossils, and when should they use profiles? A first-pass might be that because profile-oriented strategies rely on well-characterized pasts, we should expect them to be successful with sufficiently supported descriptive hypotheses. I suspect this is too quick, however: there could be virtuous feedback between how we characterize and how we explain the past. If so, however, this would need to be shown.

I want to close by drawing a few upshots.

## 5 Paleobiology as a Science of Biological Possibility

What are the historical sciences *about*? A very reasonable answer might be: *the past*. The primary epistemic benefit of historical reconstruction is knowledge of how the past actually went. That is no-doubt valuable, but I think we can say more in light of the discussion thus far. As an amuse-bouche, let's quickly consider Meghan Page's argument that historical studies can test the stability of contemporarily-established regularities:

Historical investigations often play an important and ineliminable role in advancing our knowledge of causal structure and stable regularities. When confronted with complex geological processes that occur over large regions of space and time, historical science acts as an experimental context to test the stability of currently observed regularities. As a result, historical investigations enhance our understanding of the complex causal webs that produce natural processes and help predict how such processes might evolve or shift in the future. (Page 2022, 462)

It might well be true that *given contemporary conditions*, say, there is a stable link between temperature and atmospheric carbon dioxide, but does that link project into the past or future? Under what conditions does that link remain stable? By examining the relationships between temperature and carbon dioxide across the large-scale and long-term perspective afforded by the deep past, we get to grips with the circumstances under which those conditionals might break down (see also Currie 2018, chapter 12 and Dresow 2022).

Page demonstrates how understanding the actual past can be crucial for empirically probing the robustness of the regularities we think might govern the present and future. I want to go somewhat further: we can also consider studies of the past *just as* studies of possibility. The practice of characterizing historical phenomena using traces like fossils, and then situating them across various profiles, serves to enrich our modal understanding in powerful ways. To see the point, permit me an ugly metaphor.

I've argued that the unity of *Spinosaurus* reconstruction is due to various profiles isolating and examining various properties that that central subject is taken to have. Here's the metaphor: the central subject acts as a branch around which the profiles are woven, like lights around a Christmas tree. In my discussion I've focused thus far on the tree: the 'lights' matter for illuminating the 'tree' they are attached to. But we might care about the lights themselves. Each profile is an exploration of modal space: the various ways in which secondarily aquatic vertebrates might swim, the propulsive properties of various reptilian tail designs, theropod buoyancy properties, and so on. Even if these are ultimately dead-ends regarding *Spinosaurus* reconstruction—perhaps we've just mischaracterized the phenomena, say—it doesn't follow from this that those profiles aren't themselves genuine epistemic achievements.

My suggestion is that, under the right conditions—namely, when the epistemic context is sufficiently rich—studies of profiles generate modal knowledge that are valuable independently of how the actual past went. The modality I have in mind here is pretty substantial. I don't, for instance, just mean *credence*. I don't mean that these studies only serve to provide good reason to update our subjective priors concerning some hypothesis about the actual past. This would be to say that, for instance, Ibrahim et al.'s study of dinosaur tails should make us more confident that in fact *Spinosaurus* were tail-based swimmers<sup>8</sup>. Instead, I think that (in the good case) studies

8. This is one reason that this account goes further than merely highlighting the use of models in paleobiology. It is open to say that, for instance, morphospace work like Raup's is primarily in the business of charactering a weak epistemic possibility: this is what we think is possible given what we currently know. Part of the argument sketched here claims that a more substantive conception of modal knowledge is required here.

like Ibrahim et al.'s give us good reason to think that critters of such-and-such tail-design have such-and-such capacities vis-à-vis aquatic propulsion. It is genuine modal knowledge, not simply a reduction in what we think is possible. This suggestion leaves open a bunch of epistemic and metaphysical questions regarding the nature of this modality, but for this paper I'm happy to simply say: to capture the phenomena I've analysed here, we need a sufficiently meaty conception of modal knowledge, and credence won't cut it<sup>9</sup>.

Finally, I want to draw a contrast between the explorations of possibility I've described and that more typically seen in theoretical biology. Neontological theoretical biology typically uses simple models, often grounded in evolutionary theory, to explore biological possibility (Laubichler and Müller 2007). This is often a productive way of proceeding: three-sex models of biology do a lot to explain actual sex distributions, agent-based models have shed light on the evolution of co-operation, multi-levelled selection, and so forth. However, such approaches lack something which the profile-and-central-subject-focused investigation I've highlighted have in spades: fossils.

I've argued that fossils provide epistemic grounds for linking profile-based explorations of possibility to actual biology: they have a story to tell about the *relevance* of their studies to biology that typical theoretical biology does not. This doesn't mean that such studies are *not* biologically relevant, but simply that they lack that support which fossils afford to the kinds of explorations I've discussed. If we're concerned with the abstract distance between theoretical models and the actual past, then paleobiology's 'phenomena-driven' approach should be preferred over the abstract modelling characteristic of theoretical biology (Currie 2019b).

## 6 Conclusion

The inferential and investigative strategies employed by vertebrate paleobiology are significantly more empirically sensitive, subtle and complex than the traditional view suggests. At least sometimes, fossils serve to ground reconstructions of various taxa which act as central subjects. Around these central subjects various profiles are applied, tested and constructed by isolating particular putative properties and bringing them into dialogue with relevant comparators. This is a remarkably flexible and dynamic way of proceeding which generates surprisingly productive speculation and modal knowledge. Paleobiology is not simply a science of past actuality, but one of deep possibility.

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9. For some recent discussion of fairly substantive conceptions of modal knowledge in the philosophy of science, see Massimi (2022) and Bokulich (2014).



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