

Marsupial Lions & Methodological Omnivory:

Function, Success and Reconstruction in Paleobiology

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Abstract

Historical scientists frequently face incomplete data, and lack direct experimental access to their targets. This has led some philosophers and scientists to be pessimistic about the epistemic potential of the historical sciences. And yet, historical science often produces plausible, sophisticated hypotheses. I explain this capacity to generate knowledge in the face of apparent evidential scarcity by examining recent work on *Thylacoleo carnifex*, the ‘marsupial lion’. Here, we see two important methodological features. First, historical scientists are methodological omnivores, that is, they construct purpose-built epistemic tools tailored to generate evidence about highly specific targets. This allows them to produce multiple streams of independent evidence and thus maximize their epistemic reach. Second, investigative scaffolding: research proceeds in a piece-meal fashion, information only gaining evidential relevance once certain hypotheses are well supported. I illustrate scaffolding in a discussion of the nature of functional ascription in paleobiology. Frequently, different senses of ‘function’ are not discriminated during paleobiological investigation—something which can mar adaptationist investigations of extant organisms. However, I argue that, due to scaffolding, conflating senses of ‘function’ can be the right thing to do. Coarse grained functional hypotheses are required before it is clear what evidence could discriminate between more fine-grained ones. I draw on omnivory and scaffolding to argue that pessimists make a bad empirical bet. It is a bad idea to bet against the epistemic fortunes of such opportunistic and resourceful scientists, especially when we have reason to think we will systematically underestimate the amount of evidence ultimately available to them.

1. Introduction

Historical scientists appear to operate under evidential scarcity. Signals from the past degrade over time, and the large-scale, complex nature of historical targets undermines experimental access¹. And yet historical scientists frequently provide rich, detailed and plausible hypotheses. How is such success achieved; how is so much done with so little²? I argue that two factors play an important role in explaining this surprising success.

First, historical scientists are *methodological omnivores*. Rather than specializing in a certain kind of method, a certain array of tests, or a certain set of epistemic practices, historical scientists are opportunistic: drawing on whatever resources they can, at many levels of grain, to triangulate their way to plausibility. In particular, they construct localized epistemic tools to actively generate independent lines of evidence. The importance of such lines of evidence is not news, of course: many accounts of the methodology of historical science emphasize this (see Wylie 2011, Forber & Griffith 2011 and Currie 2013). However, my discussion of omnivory supplements this by highlighting the *generation* of diverse evidence streams; that is, I focus on the plurality of methods producing independent evidence, rather than the evidence itself. As we shall see, historical scientists custom-build epistemic tools in order to generate evidence targeted at particular questions. These inferential models help maximise their evidential reach.

Second, historical science proceeds by *investigative scaffolding*: a set of claims must already be on the table for new evidence to be relevant. Investigation is piecemeal and comes in stages: both the plausibility and richness of hypotheses is built step-by-step. As scaffolds are reached, new data gains evidential relevance. This makes the epistemic situation faced look worse than it

¹ Although, see Jeffares 2008

² This is, on the face of it, a different kind of success than that which drives arguments about realism/anti-realism. That debate hinges on whether success at ‘saving the phenomena’, that is, empirical adequacy, provides reason to believe in successful theories’ posits. I am interested in how historical scientists generate the amount of knowledge that they do, given the difficulty of their investigative targets.

in fact is, as we frequently do not know what evidence matters prior to reaching a scaffold. Due to scaffolding, we systematically underestimate the possible evidence.

I illustrate scaffolding via a discussion of functional ascriptions in paleobiology. Whereas we demand that functional claims be finely discriminated in studies of extant organisms, I argue we should be more forgiving in historical contexts. This is because the evidence needed to establish fine-grained functional claims is often not available, and because a set of coarse functional claims are required to scaffold further investigation.

My aim, then, is to supplement existing accounts of the methodology of historical science, and in particular to highlight how methodological omnivory and investigative scaffolding lead us to under-estimate our epistemic potential in regards to the deep past. At the end of the paper, I draw on these points to counteract pessimism about historical science.

It is important to note that neither omnivory nor scaffolding are distinctive features of historical science: I am not in the demarcation game. Rather, they are common scientific practices which are prominent in the historical sciences because of the epistemic situations they tend to face. I appeal to these features to explain success, rather than compare sciences³. Moreover, although I compare the functional claims of paleobiologists and ‘neontologists’ (the paleobiologists’ term for biologists investigating extant targets), this also isn’t demarcation. Rather, my arguments ought to hold for anyone in the epistemically fragmented situation common to historical investigation.

My argument is built around a case study. I examine how paleobiologists have built, from fragmentary fossils, a surprisingly rich profile of the locomotion, ecology and killing behaviour of *Thylacoleo carnifex*, the so-called ‘marsupial lion’. I first introduce the case study, and then (in

³ Of course, the point of demarcation is to understand the success and failure of sciences, and so these discussions are related. However, I am not primarily interested in comparing historical to ahistorical science. Rather, I examine historical science on its own terms.

sections 3 and 4) discuss methodological omnivory and investigative scaffolding in turn, before (in section 5) arguing against pessimism.

2. *Thylacoleo carnifex*: the ‘marsupial bulldog’

Paleobiologists reconstruct organisms⁴, and this pursuit can be divided into two questions. First, the *phenotype question*: what did the lineage look like, how did it live, and how was it viable? Second, the *evolution question*: which historical forces are to blame for that phenotype’s evolution? In what follows, I discuss how paleobiologists build a phenotypic profile of *Thylacoleo carnifex*. As we shall see, evolutionary and phenotypic explanation proceed in lock-step: an organism’s phenotype and its evolutionary history are examined simultaneously. This can involve the conflation of various senses of function: I will draw on this to illustrate investigative scaffolding. Moreover, investigations of *T. carnifex* exhibit methodological omnivory: paleobiologists use custom-built, multipurpose epistemic tools to actively generate new lines of evidence. We shall also see that ‘lion’ is an ill-suited analogue for *T. carnifex*, perhaps ‘bulldog’ is more appropriate.

I will spend some time summarizing the science: this depth is necessary to illustrate the opportunism and resourcefulness of historical science. For us to see the importance and power of omnivory and scaffolding, and for my arguments about success and pessimism to hold force, we must examine scientific practice in some detail.

[Figure 1 here]

1: *Thylacoleo carnifex* skeleton from Moree (from Finch & Freedman 1988, pp 252, permission granted from CSIRO, <http://www.publish.csiro.au/nid/90/paper/ZO9880251.htm>)

⁴ Reconstructing past organisms is not the only, or even the central, business of paleobiology. More important is study of large-scale macroevolutionary patterns revealed in the fossil record.

Thylacoleo carnifex was the largest carnivorous marsupial Australia has boasted, haunting most of the Pleistocene, from 150 to 45 thousand years ago. Although *T. carnifex* was described by Owen in the 19th Century, it wasn't until the 1966 discovery of a relatively complete skeleton (see fig 1) that detailed reconstruction was possible. How do paleobiologists move from this incomplete and fragmentary evidence to a rich and plausible phenotypic profile?

I will focus on fossil rather than other evidential sources—but this is largely for convenience. As noted above, historical scientists draw on diverse lines of evidence to support their hypotheses. What we might know of *T. carnifex* certainly doesn't rely on fossilized skeletal remains alone, but also on information about their environment, non-bodily remains (trackways, coprolites and other signs), information about the ecology and atmospheric conditions of the Pleistocene, cave paintings, and so forth⁵. However, as I am interested in the plurality of method, rather than evidence-streams, it is helpful to focus on one source.

2.1 The lion's gait

One route to an organism's locomotive method is via its morphology, as we can exploit regularities between various morphological ratios and locomotion. Davis (1964) established such correlates using surveys of placental mammals. For instance, forelimb versus hindlimb length discriminates between cursors like leopards, and leapers or stotters like gazelle. Lineages with short forelimbs and long hindlimbs leap or jump, while those with equal lengths are runners. However, this doesn't discriminate between fast and slow cursors. The humero-radial index (the ball-and-socket joint in the 'elbow') does, however. So, by triangulating between different indices we can infer locomotive method. Davis took this a step further by constructing a 'generalized mammal': a fictional mammal who sits in the centre of the morphological indices. Roughly, a

⁵ For instance, Carrie et al 2011 describes a trackway assemblage from Victoria which may contain a few traces of *T. carnifex*, however this is quite speculative.

mammal of those proportions is partway between a cursor, a fossicker, a jumper, and so on. An actual animal's locomotion is indicated by its divergence from the generalized mammal.

Finch & Freedman (1988) apply this idea to *T. carnifex*. First, they establish *T. carnifex*'s morphological index profile from detailed measurements of the Moree specimen. Second, they take similar measurements of eleven extant Australian marsupials. Third, they draw on Davis' generalized mammal. By comparing *T. carnifex* to the placental and marsupial data, they infer its locomotive method.

[Figure 2 here]

2: Body proportions on various indices for (a) Davis 1964's 'generalized mammal'; (b) The marsupial lion; (c) common wombat; (d) southern brown bandicoot. Divergences between the generalized mammal and targets are inroads to their locomotion (from Finch & Freedman pp 262 permission granted from CSIRO,

<http://www.publish.csiro.au/nid/90/paper/ZO9880251.htm>)

The placental data is more conclusive than the marsupial contrasts. Although on many indices *T. carnifex* is similar to the Tasmanian devil "... and by comparison with the hypothetical 'generalized' condition, suggest a moderately fast cursorial locomotion (pp 269)", on some important indices *T. carnifex* is koala-like. The marsupial data, then, suggests *T. carnifex* was either a climber⁶ or a cursor:

The increased length of the femur, relative to the tibia in both the marsupial lion and the koala suggests that the long hindlimb is associated with the exertion of considerable force. The elongate radius of the two animals could be an adaptation to speedy locomotion, climbing or feeding (269).

⁶ The thought that *T. carnifex* was arboreal can be traced to Wells & Nichols (1977)'s morphological study. My philosophical point does not rely on which hypothesis about *T. carnifex*'s locomotive method turns out to be the most plausible: indeed, if I am right about scaffolding, we ought to expect debates like this to drive further discovery.

Finch & Freedman reject the climbing hypothesis as it is not viable for an organism of *T. carnifex*'s size to climb as a koala does⁷. They suggest a different function:

The koala's use of its limbs in climbing vertical column lengths would suggest that the latter animal is too large to 'bound' up a tree. Also as the only clear similarity in limb ratios between the marsupial lion and the scansorial *T. vulpecula* lies in the R/H ratio... it is not likely to indicate a common climbing habit but to imply a cursorial locomotion and the use of the forelimb in handling food (269).

Finch & Freedman, then, take measurements of *T. carnifex* and compare these to both placental and marsupial measurements. They use what I will call a 'bracketed model' to infer the marsupial lion's locomotive behavior from the measurements. Where these inferences are ambiguous, they consider the hypotheses in terms of viability. They conclude:

Limb ratios therefore lead to the conclusion that *Thylacoleo* was a cursor of medium speed. Its powerful hindlimbs suggest that it could have pounced on its prey while the long forelimbs were probably used to hold the food and draw it towards its jaws (270).

It is unclear whether Finch & Freedman's claims about the functional morphology of *T. carnifex* should be taken as reconstructions of the phenotypic profile of the Moree specimen, or of the specimen's evolutionary history, or both. At times the limbs are referred to as adaptations, meaning the traits were selected for that purpose, while at other times evolution is not mentioned. As I discuss in more detail in section 4, in neontological contexts it is essential to distinguish between senses of function which appeal to an organism's evolutionary history, and those which do not. Later on, I partially vindicate such functional conflation, due to its role in

⁷ Recently, Wells et al 2009 have argued that *T. carnifex* was a climber after all, pointing to pedal morphology. As they discuss, heavy animals like bears and gorillas can certainly climb trees. This misses the mark: Finch & Freedman's complaint is not that something as large as *T. carnifex* couldn't climb a tree, but that it couldn't climb a tree in a koala-like manner. Especially in light of Wroe et al 1999's weight estimates, I think this fairly convincing.

investigative scaffolding. Let's move to another example, where different epistemic tools are constructed to access *T. carnifex*'s past.

2.2 The lion's bite

We can infer carnivore ecological role by exploiting correlations between bite force and body size. Bite force can be calculated for both extant and fossil mammals using the 'dry skull' method. Skull dimensions and jaw muscles are modelled as a simple lever⁸, and taking maximal bite force as a function of bending stresses across the jaw. Thomason (1991) develops the idea, calculating how much 'bending' stress a skull undergoes, and from that an organism's maximal bite force.

Here is Thomason's equation for calculating bending stress (σ):

$$\sigma = \frac{Fd}{I/y}$$

Bending stress is a function of the *bending moment*, the maximal bilateral biting force at a point in the teeth row (F), and the distance between that point and the length of jaw under consideration (d); and the *moment of bending resistance*, which consists of the vertical distance between the centroid⁹ of the length of jaw under consideration to its surface (y) and the second moment of area of that length of jaw (I). Basically, the numerator in the equation (the bending moment) is the stress on the skull. The denominator (the moment of bending resistance) is the skull's capacity to resist that stress.

⁸ See Thomason (1991) for extended discussion of the idealizations made, and their justifications (in particular, estimations using beam-theory are contrasted with independent *in vivo* tests of bite force).

⁹ The *centroid* of a two dimensional object is (informally) the point at which it would, were it a cardboard cut-out, balance perfectly on the tip of a pencil.

[Figure 3 Here]

3: (a) *D. virginiana* skull showing masticatory forces; (b) the moments of the forces (see text for explanation)

(from Thomason 1991, pp 2328, NRC research press)

Figure 3 compares the skull of a Virginia opossum (*Didelphis virginiana*) (a) and its subsequent bite force (b). **C** is the bite force at the canine, **R** is the reaction force at the temporomandibular joint and **M** is the force which disperses from the adductor musculature. **X** in (b) marks the approximate location of maximal stress on the skull.

Wroe et al (2005) estimated the canine-centred bite force for a group of carnivores including representative felids, canids, hyaenids and others. They then plotted raw bite force against body mass to determine *Bite Force Quotient* (BFQ), as seen in figure 4:

[Figure 4 here]

4: BFQ (bite force against body mass) for felids (open triangles), canids (grey filled triangles), dasyuromorphians (grey filled squares), thylacoleonids (black filled squares), hyaenids (grey filled diamonds), thylacosmilids (open squares) and others (grey crosses). *T. carnifex* is circled. (from Wroe et al 2005, pp 620, permission granted from RSP)

Wroe et al then match BFQ to behaviour in extant animals. I will focus on correlations relating to feeding ecology:

Our results demonstrate that among living mammalian carnivores, BFQ is a broad indicator of relative prey size and feeding ecology (623).

Roughly speaking, the higher the BFQ, the bigger the relative prey size. Hypercarnivores such as wild dogs and wolves bring down organisms much larger than themselves, and consistently have high BFQ. Bears rarely eat anything bigger than a salmon, and have low BFQ. *T. carnifex* has impressive BFQ: its bite equals the raw force of an adult African lion, despite being half the body-length. Wroe et al take this as evidence for hypercarnivory, speculating they may have preyed upon "... sub adults of the heaviest available prey..." (624): the multi-ton *Diprotodon*.

Here, Wroe et al exploit both the biomechanical properties of skulls, and ecological regularities across mammalian carnivores. They construct epistemic tools to do so. Once a plausible picture of *T. carnifex*'s ecology is on the table, Wroe et al are then in a position to speculate about hunting behavior—their investigation is scaffolded. Combining tooth morphology with bite force suggests a killing method. *T. carnifex* has the largest vertical shearing 'carnassial' cheek-teeth of any known carnivore (see fig 5 & Werdelin 1988). The combination of such teeth, and their impressive bite force,

... may have enabled *T. carnifex* to rapidly slice through tracheas or vital blood vessels and quickly dispatch large, potentially dangerous prey, although mechanical simulation will be required to confirm this (624).

[Figure 5 here]

5: skull of *T. carnifex*, showing 'carnassial' cheek teeth (Source: Wikipedia

http://en.wikipedia.org/wiki/Marsupial_lion)

Wroe et al use biomechanical theory to estimate *T. carnifex*'s bite force. This measure, combined with body size, determines BFQ. BFQ is then matched to prey size, allowing them to infer the marsupial lion's ecological role. Wroe et al then draw on aspects of *T. carnifex*'s phenotypic profile, BFQ and tooth morphology, to hypothesize killing style, and propose further tests.

We have shifted from the fragmented bones of the Moree specimen, to a rich and plausible profile. *T. carnifex* was a medium-speed cursor, killing large prey. Unlike big cats, which kill larger prey by suffocation, *T. carnifex* had the bite force and the carnassial molars required to dispatch large and dangerous animals quickly. Part of the explanation for this epistemic success is an increase in the number and quality of fossils, but perhaps more important is the generation of new evidence by designing new techniques and tools: methodological omnivory. I will cover one more study before turning to my analysis.

2.3 The lion's skull

Goswami et al (2010) create a skull morphospace by digitizing extant and extinct carnivore skulls and plotting them along several dimensions of transformation. The dimension PC1, for instance, shifts from a wide skull to a long thin one (see the wire frames in figure 6). PC1, like BFQ, tracks hypercarnivory in non-felids. Bear-like and cat-like animals fall to the left, while dog-like hypercarnivores cluster slightly over the mid-point. *T. carnifex* fits squarely within 'dog space', further evidence of hypercarnivory. Goswami et al, then, exploit correlations between skull shape and ecological role to build on *T. carnifex*'s phenotypic profile. However, phenotype reconstruction is not all Goswami et al are interested in: they also explore the evolution of carnivory. This demonstrates the multi-purpose nature of the epistemic tools historical scientists use, and the coupling of phenotypic and evolutionary reconstruction.

[Figure 6 here]

6: Two of Goswami et al's dimensions of skull morphospace (permission from RSP)

First, Goswami et al test a hypothesis about marsupial developmental constraints. Marsupial carnivores have fared badly faced with placental competition. *Prima facie*, marsupial carnivores in South America, Australia and elsewhere were outcompeted by invading placentals: for instance the displacement of thylacines by dingos¹⁰. Goswami et al discuss two possible explanations, both involving developmental constraints which lower marsupial, but not placental, evolutionary potential. On one, the requirements of neonate suckling restricts skull shape. Marsupials are born earlier than placentals and the requirements of early suckling could restrict viable skull shape. Placentals suckle later in development, and without this restriction could occupy ecological roles more efficiently. Another hypothesis blames marsupial dental development. Marsupial molars

¹⁰ Leah Schwartz has pointed out to me that things are not as cut and dry as they appear: whether such out-competition really occurred is difficult to establish. I don't think this undermines the philosophical point of the discussion, however.

erupt at a single point, the molars shifting backwards like a conveyor-belt as new teeth emerge. As a result, all marsupial molars are carnassial. By contrast, placental molars erupt at several locations, allowing for greater dental specialization. If the first hypothesis is right, we should expect placental carnivore skull disparity to outdo that of marsupials. However, this is false:

... disparity of metatherian and eutherian carnivores was... near equal and not significantly different... This result suggests that the marsupial mode of development has not constrained the morphological evolution of the cranium in marsupial carnivores (Goswami et al, 7-8).

Goswami et al take this as reason to reject the first hypotheses in favor of the second¹¹. They also use their model to examine convergences in skull shape across carnivores. In Figure 6 placental carnivores are represented pictorially, and marsupials with letters. There are several letters in 'dog space', but none in 'cat space':

... 'dog space' has been converged upon independently by at least four lineages of metatherian carnivores. By contrast, it appears that 'cat space' has been left relatively unexplored by extant or extinct metatherian carnivores, despite the frequent application of felid common names to metatherian carnivores, such as the marsupial lion and native cat (Goswami et al, 7).

Not only does Goswami et al's model support hypotheses about *T. carnifex*'s phenotypic profile, it also tests claims about marsupial developmental restrictions and identifies patterns of evolutionary convergence.

These three studies, taken in combination, provide a surprisingly plausible, rich picture of *T. carnifex*. 'Marsupial lion' is, perhaps, a misplaced moniker. *T. carnifex* was heavy, stocky, and killed large herbivores using its crushing bite. More like a bulldog or a hyena, then. In the

¹¹ However, Bennett & Goswami (2013) have since produced further evidence of less disparity across marsupial skulls than placental skulls.

remainder of the paper I aim to answer just how paleobiologists draw detailed phenotypic profiles from incomplete remains.

3. Methodological Omnivory

Historical scientists are methodological omnivores: they maximize the epistemic potential of fragmentary remains by constructing specialized epistemic tools. As mentioned in the introduction, an essential part of historical hypotheses' support comes from convergence from multiple evidence streams. Where such consilience matters, and it undoubtedly does when evidence is fragmentary, generating such lines of evidence is imperative.

An investigation is omnivorous when it utilizes multiple and disparate methods to generate evidence streams: the most interesting cases being when inferential and explanatory tools are custom built for the purpose at hand. These epistemic tools are common in paleobiological reconstruction, as illustrated by *T. carnifex*. Historical scientific investigation proceeds, at least sometimes, by working out what inferential work can be done with the available evidence and the applicable regularities. New evidence is discovered by opportunistically exploiting what resources are available, and this explains how so much is achieved with so little.

Methodological omnivory should be understood in terms of the 'disunity' of science. This cluster of views rejects the idea that science aims for unified theories, instead seeing it as a more-or-less integrated patchwork of models, techniques, theories and so forth. Omnivory has significant parallels with Wylie's (1999) emphasis on scientists' exploiting of disunity and Mitchell's 'integrative pluralism' (2001, 2003). Mitchell's integrative pluralism focuses on how non-equivalent models can be integrated to provide sufficient, but theoretically disunified explanations of local phenomena. Her view and mine are distinct. First, for Mitchell, disunity's source is the nature of modelling, the trade-offs involved in idealization, and complexity, whereas methodological omnivory is driven by incomplete data. Second, Mitchell is mostly interested in

how models and theories generate explanations of phenomena, while I am interested in how evidence is generated. Methodological omnivory and integrative pluralism are both interested in how scientists exploit disunity, but have different focuses. The two are, surely, complimentary.

In what follows, I characterize three schematic tools which paleobiologists adapt and apply to reconstruction. This analysis illustrates the power and flexibility of paleobiological investigation—in section 5, I draw on this to argue that pessimists about our potential to discover many facts about the past make a bad bet.

3.1 Bracketed Models¹²

The stars of *T. carnifex* reconstruction are *bracketed models*¹³. A bracketed model exploits correlations between phenotypic traits across phylogenetic groups. For instance, in mammals different morphological indices track locomotive method; in mammalian carnivores both skull shape and BFQ track ecological role. Bracketed models have the following schematic form:

In phylogenetic grouping w (in environment x^{14}), trait y and z are coupled, that is, lineages with trait y are likely to have trait z and vice-versa, unless exceptions $e_1, e_2, e_3 \dots e_n$ hold.

Bracketed models are *ceteris paribus* on two counts. First, they are restricted to a particular phylogenetic group. Wroe et al make no claims about whether the BFQ→ecology inference is sound in birds, reptiles or fish. Bracketing restricts the model's scope to close relatives, as shared ancestry should track shared characteristics. Second, the models may exclude atypical cases within the phylogeny. For instance, Wroe et al exclude abnormal cases from their model. The

¹² In Currie (2013) I call these 'parallel models', as in that context I am emphasize the role of homoplasies in their inferences.

¹³ 'bracketed', in reference to 'phylogenetic bracketing'.

¹⁴ Thanks to Brett Calcott for suggesting the inclusion of the environment. Although the bracketed models considered in *T. carnifex* reconstruction do not index inferences to environments, some do. Particularly in cases where evolutionary convergences are exploited to support adaptationist hypotheses (see Currie 2013).

aardwolf's BFQ matches some bears and smaller cats, and "Although this finding is consistent in that all take relatively small prey, it does not reflect the fact that the *P. cristatus* subsists largely on termites" (623). The inference's stability depends on the typicality of the specimen: "... BFQ may not directly reflect feeding ecology for morphologically atypical taxa that do not fit within generalized biomechanical models" (623).

Bracketed models are not merely 'calculation tools', geared only towards predicting phenomena. First, their plausibility is not only derived from success across extant samples, but from evolutionary theory. Phylogenetic bracketing assumes that closely related lineages will express similar traits in similar circumstances. When inferring between homologues, it is thought likely that a lineage's traits will be present in close relatives. This requires 'phylogenetic inertia' (Griffiths 1996): over time, traits are retained more often than not. Evolutionary theory supports this as robust heritable signals are required for evolution to forge complexity (Levy & Currie 2014). Inferences based on homoplastic parallelisms (Currie 2013, Powel 2012) assume that closely related organisms will converge on similar traits in similar environments: roughly, they come to the same solutions to environmental problems. It is thought that as closely related lineages share developmental and phenotypic resources, they are more likely to respond similarly to selective pressures.

The strength of this point depends on how determinate the relationship between trait and environment is; and this is a matter of significant contention. Beatty & Desjardins (2009), for instance, discuss ways in which historicity can undermine selection (see Turner 2011 for a summary of contingency in paleobiology). Natural selection works with what it has; that is, it builds on pre-existing forms. Its influence, then, is path dependent on previous phenotypes. Moreover, both chancy mutations, and the order of mutations, can influence evolution's direction. I would be astonished if there was a general answer to history's effect on natural selection, and it would take us too far afield to discuss this in any detail. Bracketed models do not

necessarily make adaptationist assumptions. When they do, suffice to say, if the models' phylogenetic scope is relatively constrained, the *shared* history of the lineages should partly counteract contingency. Moreover, bracketed models can be rigorously and carefully tested. Davis' generalized placental mammal is constructed from an extensive survey, and Finch & Freedman combine it with the morphological characteristics of a broad group of marsupials. A bracketed model's licence is underwritten both by tests, and by evolutionary theory. Finally, the purpose of such models is to provide some *inferential grip*, not certainty. Of course it is possible that *T. carnifex* is an outlier, that historicity tripped up the model, but nonetheless Finch & Freedman's study provides legitimate grounds for cursorial locomotion in that lineage.

Second, bracketed models are explanatory. Goswami et al's skull morphospace does not merely ground inferences from morphology to ecology, but explains why organisms have the skulls they do. Felid skull and tooth morphology facilitates choke holds. Most of their bite force centres on the canines in order to clamp shut, and their molars are heavily reduced to accommodate their prey's necks. Their relatively constrained skull-shape disparity compared to other *Carnivora* suggests that it is constrained by the requirements of choking.

Bracketed models, then, exploit regular couplings across phylogenetic groups. These couplings can be determined by examining extant animals, but are also granted plausibility from evolutionary theory: we should expect closely related organisms to evolve in similar directions in reaction to environmental stimulus. Bracketed models are multi-purpose tools. They allow us to build phenotypic profiles, and they ground explanations. Additionally, they are an empirical inroad to evolutionary questions. Goswami et al use their model to infer the ecology of extinct carnivores, but also use it to test hypotheses about marsupial evolvability, and identify convergences between placental and marsupial lineages.

3.2 Biomechanical Models

Paleobiologists do not only exploit regularities across phylogenetic groups: they also use 'biomechanical models', which take measurements as inputs and output morphological and physiological capacities. Wroe et al's means of calculating maximal bite force is one such model. By treating the skull as a lever, inferences can be made on the basis of mechanics. Organic materials are subject to mechanical principles just as surely as the more traditional stock and trade of engineering. For instance, this approach is used to estimate top speeds in extinct lineages. As Turner (2009) details, simulations of *Tyrannosaurus rex* are used to infer maximal pace. These models draw on both fossil and comparative evidence to construct a digital dinosaur. Engineering principles about the strength and stresses of materials are then used to establish top speed.

Like bracketed models, biomechanical models rest on a bed of evolutionary theory. Comparative data is used: bite force calculations are compared to *in vivo* tests with extant organisms. Homologous inferences are required to apply mechanical calculations to extinct organisms. Also, of course, the basic engineering and mechanical inferences rely on the background theories of those sciences. The toolkit of engineering is exploited to extend and enrich phenotypic profiles.

It is worth pausing here to compare biomechanical models with optimality models. An optimality model explains phenotype in terms of engineering trade-offs between traits, ignoring history and chance. For instance, it may be that there is a tension between, say, optimal running pace in a *T. Rex* and optimal absolute size. Larger *T. rex*, perhaps, are better at dispatching prey, while faster *T. rex* are better at catching prey. An optimality model would represent size and speed in terms of payoffs and explain actual *T. rex* phenotype as the local optima between them. The precise role, and the worth, of optimality modelling is extremely contentious (see Potochnik

2009)¹⁵. Biomechanical models, by contrast, do not appeal to optimality, but rather the inferred mechanical properties of the organism in question. This requires significant idealization (*T. carnifex*'s jaw is not a lever!), but these idealizations are not to emphasize natural selection. Rather, they abstract from any historical information, and simply consider what something of those materials could do. Optimality models are, however, sometimes used in viability analysis.

3.3 Viability Analysis

Both bracketed and biomechanical models provide rich phenotypic profiles. These are further extended by *viability analysis*. Roughly, a viability analysis asks what an organism with the phenotypic profile in question needs to survive and reproduce. These can be informal and linguistic or more formal. Finch & Freedman use an informal viability analysis to conclude that *Thylacoleo carnifex* was a cursor rather than a climber; an animal as large as the marsupial lion couldn't climb in a koala-like manner.

More formal viability analyses are common in debates about the functional morphology of sauropod necks. It is controversial whether sauropod stance was giraffe-like with raised neck, or instead held at shoulder height (although I suspect that a consensus is developing: some phylogenetic groups stood upright, while others kept necks at shoulder-height, see Christian & Dzemski 2011). Anti-neck-raisers appeal to engineering models to argue that sauropods lacked sufficient bracing for upright heads (Martin, Martin-Rolland and Frey 1998), physiological models suggesting that sauropod hearts would be unable to supply raised heads (Seymour 2009), and

¹⁵ For instance, there are many ways of getting around trade-offs and this can make optimality models misleading. Erickson et al 2004 have argued that *T. rex* had two distinct ontogenetic stages: a juvenile stage characterized by fast running speeds and feathers, and a slow, featherless adult packing a major bite. They speculate that the animal hunted in packs, the smaller animal catching and harrying prey, allowing their mature conspecifics to catch up for the kill. If there is a tradeoff between size and speed in *Tyrannosaurids*, this is a way of solving it: although I doubt it would be represented in an optimality model.

optimality models which show that shoulder-height grazing is an efficient way of maximizing browsing range while minimizing movement (Ruxton & Wilkinson 2011).

Viability analyses, then, take many forms. The basic shape, however, is something like this:

Organisms with phenotypic profile p (consisting of traits $t_1, t_2, t_3, \dots, t_n$) require trait t^* for viability, or would be unviable if they expressed t^{**}

Paleobiologists consider the organism as a working whole, and this allows them to support and exclude hypotheses. Parts of a phenotypic profile ‘force’ others: something as big as *T. carnifex* cannot climb as a koala does. As we shall see, viewing the organism as a working whole in part explains the scaffolded nature of paleobiological investigation. It is only once a fairly rich phenotypic profile is on the table that we can exploit the relationships between aspects of that profile to extend our reach. The restrictions body mass places on koala-like climbing only became evidentially relevant to *T. carnifex* reconstruction once Finch & Freedman’s bracketed model had done its work.

The capacity to construct targeted, local models allows scientists to build and support rich phenotypic profiles from minimal remains, in section 5 this will be drawn on to explain paleobiological success and respond to pessimism. Before that, I to shift to investigative scaffolding via a discussion of ‘function’.

4. Functional ascription in paleobiology

As we have seen, when reconstructing phenotypes, historical scientists draw on both evolutionary theory and hypotheses about evolutionary history. Bracketed and biomechanical models rely on background theory from natural selection and phylogenetic inertia. Viability models, too, lean on evolutionary theory. Bracketed models sometimes play dual roles: exploring phenotype and evolution simultaneously. It isn’t that surprising, then, that in phenotype

reconstruction historical scientists appear to play fast and loose with functional claims, slipping between explanations of an organism's evolutionary history and its phenotype. In this section I explain and vindicate this behaviour, as well as illustrate investigative scaffolding.

Many philosophers of biology and mind think that traits play a plurality of functional roles¹⁶. Although this literature is rich and sophisticated, for my purposes I only need a rough distinction between two categories of function, and two corresponding types of explanation. Call one sense of function *etiological*: for a trait to have a particular function, it must have played that role in the history of the lineage in question. We provide *evolutionary explanations* by appealing to those functions. For instance, if *T. carnifex*'s carnassial was an adaptation for shearing through bone—if that adaptive advantage explains the trait's presence—then it has that etiological function. Call the other sense *causal-role*: for a trait to have a particular function, it must play that role within some system, irrelevant of whether it has in the past, or whether it was 'designed' to play that role. Causal-role functions can underwrite *viability* explanations which explain how a trait aids an organism's survival and reproduction in a particular context (Wouters 1995). If *T. carnifex*'s carnassial evolved for a purpose other than bone-shearing, but was a by-product put to use in that way, then it has that causal-role function.

These two categories of function are an essential part of the neontological toolkit. An aspect of Gould & Lewontin (1979)'s anti-adaptationism is the complaint that adaptationists fail to distinguish between them (see Forber 2009). Hasty adaptationists read causal-role function as etiological function. This matters. Although contemporary phenotype provides an inroad to evolutionary history, the road is rutted. Adaptationist explanations posit the emergence of traits in response to past selective environments. In assigning adaptive function to traits, then, we

¹⁶ See, for example, Brandon 2013, Amundson & Lauder 1994, Griffiths 2006, Cummins 1975, Preston 1998.

need to match the trait's emergence to an environment. This can be done, but the inference is far from simple.

Because etiological and causal role facts come apart both in principle and practice, there is *prima facie* reason for concern about their apparent conflation in paleobiology. Recall Finch & Freedman's discussion of *Thylacoleo carnifex*'s hindlimbs. Their bracketed model didn't discriminate between an arboreal, koala-like animal and a cursorial, devil-like one. As they put it,

The elongate radius of the two animals could be an *adaptation* to speedy locomotion, climbing or feeding (269, italics mine).

Why, in reconstructing the phenotype of an organism, would Finch & Freedman speak in adaptationist terms? If the limbs are adaptations for climbing, they must have evolved for that purpose in response to environmental pressures faced by *T. carnifex*'s ancestors. Surely, when asking the phenotype question, evolutionary claims should be put aside. Indeed, from the mouths of neontologists such talk is problematic, as we expect them to keep their functional ducks in a row. Naively shifting from a trait's viability to its evolutionary role ignores confounding hypotheses: traits can be exaptations, by-products, or developmental quirks. Indeed, Finch and Freedman seem open to just this criticism. Why think *T. carnifex*'s hindlimbs evolved due to selection for cursorial motion and that the function was retained in their specimen? Why not think they are vestiges, or exaptations, or whatever else?

I will not claim that phenotypic and evolutionary reconstruction are always coupled. I suspect that surveying functional ascriptions over a wide variety of paleobiological reconstructions would reveal a fair amount of slippage, but I don't want to pursue such a survey here. First, because I suspect that any particular survey would be all too easily accused of cherry-picking. Second, my argument does not rely on paleobiological practice, but on epistemology. I argue that, as opposed to (most) neontological investigations, in paleobiology slippage between different kinds of function is (sometimes) not problematic. This is because, epistemically speaking, phenotypic

and evolutionary reconstruction are coupled: first because of a lack of discriminating evidence; second because of investigative scaffolding.

4.1 Loci of Uncertainty

Compare neontological and paleobiological investigations of function. The neontologist, it seems, has an easy task and a hard task. Determining the causal-role facts is relatively straightforward, as it is typically amenable to direct investigation. For instance, we know that big-cat dental morphology facilitates their distinctive killing style, because we have seen them at work. The neontologist's hard task is determining the etiology facts. Did the dental morphology evolve for suffocating prey, or was it the happy outcome (for cats at least) of some other evolutionary function? To determine this, we must investigate the history of the lineage, reconstruct their ancestors, work out when, and in what sort of critter, the dental morphology evolved, and so on. The paleobiologist, by contrast, has two difficult tasks. Determining both causal-role and etiology facts involve difficult, complex inferences from fragmentary evidence. Most of the time, neontologists have little difficulty answering the phenotype question: after all, they can go and look. The evolution question is less certain. For paleobiologists there are two loci of uncertainty: both phenotype and evolution questions are tricky.

This difference, I think, justifies functional slippage in paleobiology. Much of the time paleobiological evidence does not discriminate between etiology and causal-role function. Consider the hypothesis that *T. carnifex*'s distinctive carnassial teeth evolved in order to slice through tracheas; the hypothesis that they are an exaptation, evolving for some other purpose and then being put to trachea-slicing work; and the hypothesis that they were a vestigial trait: some *T. carnifex* ancestor used them for that purpose, but *T. carnifex* did not. It seems as if Wroe et al's evidence, bite force and tooth morphology, speaks equally for all three hypotheses. Such evidence gives us reason to believe that, somewhere along its evolutionary history, *T. carnifex* or

its ancestors were using the carnassial teeth for slicing, but it does not identify where within that history. Much of the time, the fine-grained information about trait-emergence and environment-correlation needed to discriminate between such hypotheses isn't available.

Sometimes paleobiologists cannot empirically discriminate between the etiological and causal-role facts. If so, then paleobiologists have no pressing reason to make that distinction¹⁷. There is a more optimistic rationale for functional conflation as well: it can be necessary for discriminatory evidence to become relevant. Let's turn to that now.

4.2 Investigative Scaffolding

A further justification for paleobiological ambiguity about function is due to what I call *investigative scaffolding*. In brief, in order to discriminate between some functional hypotheses, a set of coarse hypotheses must already be on the table. Once these are established (or near enough) further tests become relevant. The scaffolded nature of investigation partly explains our surprise in paleobiological success. We tend to underestimate the epistemic resources available, as not all ultimately relevant evidence is discernible prior to reaching a scaffold.

Recall Finch & Freedman's use of comparative marsupial evidence to reconstruct *T. carnifex*'s gait. The results of their bracketed model were ambiguous: *T. carnifex*'s hindlimbs indicated either a devil-like cursor or a koala-like climber. This study reached a scaffold: although it did not distinguish between cursor and climber, it did show that, for instance, *T. carnifex* did not fossick like a wombat. Once the scaffold was reached, new evidence became relevant: in this case, the size limits imposed by koala-like climbing. By appealing to this (informal) viability model, Finch &

¹⁷ A referee points out that that, if pessimists are right and many facts about the past will remain unknown to us, then this defence of functional conflation will be much stronger. There is, then, something of a tension between my argument against pessimism, and my argument that a lack of information about the past can justify conflation. If the former argument is right, the scope of the latter argument will decrease. I don't see this tension as problematic: even the most optimistic attitude to the historical sciences ought to allow that, at least sometimes, the past will remain hidden—and in those cases, some conflation might be allowable.

Freedman further extended their epistemic reach. The relationship between koala-like climbing and body size only became relevant after the bracketed model had done its work. Historical science progresses via such scaffolding: new empirical data becomes relevant as new hypotheses are supported. This explains, and vindicates, functional conflation in paleobiology.

Sometimes paleobiologists collapse etiological and causal-role claims as a result of scaffolding. Functional discrimination is carried out from a scaffold of what I will call *disjunctive functional hypotheses*. These should be read as well-established claims of the form ‘trait *t* has etiology function *f* or *t* has causal-role function *f*’. These claims are typically asserted either with the simple ‘*f*’ (*T. carnifex*’s long hindlimbs are for pouncing’) or by asserting one of the disjuncts (*T. carnifex* used its long hindlimbs to pounce’/*T. carnifex*’s long hindlimbs evolved for pouncing’). I suggest that we read many paleobiological function ascriptions as the assertion of disjunctive functional hypotheses. These need to be on the table for discriminatory evidence to become evidentially relevant.

What if the historical scientists are not interested in one or the other sense of function? Imagine Finch & Freedman only cared about providing adaptationist explanations of *T. carnifex*. If so, isn’t it the case that the causal-role facts are subservient, and so they are not conflated? I don’t think so: investigative scaffolding doesn’t turn on the intentions of the researcher. Even if we are only interested in whether *T. carnifex*’s long hindlimbs evolved for pouncing, supporting that hypothesis requires discriminating it from the possibility that it evolved for some other purpose, and pouncing is a by-product. In that case, pouncing would be a function by the causal-role facts, but not the etiology facts. Even if my interest is more towards the phenotype question, or the evolution question, scaffolds are still required.

And so, paleobiologists sometimes need to collapse historical and ahistorical functional claims in order to later discriminate between them. If they are at that earlier stage, we should

read function-talk disjunctively. Of course, once the scaffold is reached, and if such claims can be empirically discriminated, then paleobiologists ought to pull the disjuncts apart.

To be clear, my argument does not distinguish paleobiologist from neontologist, but turns on epistemic circumstances. In one circumstance, the phenotype question is easy while the evolution question is hard, and in the other both questions are difficult. Some neontological circumstances fit the latter better than the former; as being extant doesn't guarantee easy recovery. For instance, some organisms, such as the denizens of deep oceans, are extremely difficult to investigate; the causal-role functions of complex, population level phenomena are difficult to establish. In these circumstances, we ought to expect similarly scaffolded investigations. Moreover, in paleobiological circumstances with rich evidence we should expect investigation to proceed in a more 'neontological' fashion.

Moreover, paleobiologists do not get a free pass on functional ascriptions. In fact, my account provides an (albeit rather abstract) criteria for discriminating between legitimate and problematic functional conflation. In brief, we should forgive conflation and adopt my disjunctive reading when either (1) available evidence does not speak to functional difference, or (2) when a disjunctive scaffold is required for discriminatory evidence to gain relevance. When neither condition is met: if there is such evidence, or some has been generated via scaffolding, biologists ought to make finer-grained distinctions.

With methodological omnivory and investigative scaffolding on the table, I close with a brief discussion of how these explain the success of historical science, and what the consequences are for our attitude towards them.

5. Pessimism & success in historical science.

Both philosophers and scientists, faced with the incompleteness of the historical record and limited experimental access, sometimes adopt a pessimistic attitude about our capacity to uncover the past. Here are some examples. Wylie (1985) describes the history of archaeology as marked by a tension due to pessimism. Archaeologists see their access to the past as sketchy, at least compared to ‘experimental’ scientists such as chemistry. According to Wylie, this leads to two extreme reactions: on the one hand an over-cautious empiricism, on the other a free-for all subjectivism. In paleoanthropology, Lewontin’s objections to reconstructions of the evolutionary history of hominid cognition are representative:

History, and evolution is a form of history, simply does not leave sufficient traces, especially when it is the forces that are at issue. Form and even behavior may leave fossil remains, but Natural Selection does not. It might be interesting to know how cognition (whatever that is) arose and spread and changed, but we cannot know. Tough luck (Lewontin 1998, 132).

Turner’s *Making Prehistory* (2007, see also 2005) is the best developed of this kind of view. In brief, he argues that appeals made in support of scientific realism—the capacity to conduct repeated experiments, for instance—are much less applicable to the historical sciences. Part of his argument turns on what epistemic resources are available. Given the destruction of many of the past’s traces, and moreover that our background theories about historical processes lead us to expect this destruction, Turner bets that historical scientists will often have insufficient evidence:

Although they can develop new technologies for identifying and studying potential smoking guns... historical scientists can never manufacture a smoking gun. If, in fact, every single dinosaur heart was destroyed by the fossilization process there is nothing anyone can do about it (Turner 2007, 58).

Although there is not space here to fully respond to Turner's position, methodological omnivory and investigative scaffolding provide reason to think that he (and other pessimists) are too hasty. To see why, I'll first make explicit how they explain the success of historical science.

The capacity of historical scientists to provide rich, plausible hypotheses is surprising when we consider how indirect our access to the past is, and how fragmentary our evidence is. Omnivory and scaffolding suggest that our access is much richer than it first appears. They are not the whole story, of course. Historical scientists exploit dependencies between past events (Currie under review), draw on multiple streams of evidence, experimentally test and support background theories (Kosso 2001, Jeffares 2008), and rely on common cause explanations (Cleland 2011, Tucker 2004). However, methodological omnivory suggests that more can be done with remains than meets the eye, and investigative scaffolding suggests that we will underestimate available evidence. Let's take each in turn.

Methodological omnivory, in particular the generation of evidence using custom built tools like those used to reconstruct *T. carnifex*, explains how historical scientists draw rich, plausible hypotheses from scant remains. They maximize inferential reach by bringing together a disparate group of techniques and methods and opportunistically constructing targeted models. Moreover, subsequent hypotheses gain plausibility via their role in the overall profile. The support behind reconstructions of *T. carnifex* are not only due to the well-grounded and diverse techniques drawn on in its reconstruction, but because of how the profile hangs together. *T. carnifex* has had skin, muscle, behaviour, and an ecology layered over its bones, and part of the hypothesis' plausibility comes from the viability of the organism as a living, breathing critter. These creative ways of generating lines of evidence show that historical scientists have more epistemic resources than it appears if we understand their practice in overly simplified terms.

Historical investigation is scaffolded: some evidence is only relevant once other hypotheses are on the table. Positions like Turner's require betting that there will frequently be past

hypotheses for which there is insufficient evidence, on the grounds that we ought to expect the relevant traces to have decayed. However, it is not clear how we can tell what evidence will matter *prior* to scaffolds being reached. That is, investigative scaffolding implies that epistemic fates are opaque, and opaque in a particular direction: the total evidence prior to a scaffold is less than the evidence which could be available once that scaffold has been reached. This, then, gives us reason to think that we will systematically underestimate the amount of evidence available for some historical target. After all, I doubt many would expect that size restrictions on koala-like climbing would be evidentially relevant for reconstructing the gait of *T. carnifex*.

Pessimism requires that we have a good handle on how much evidence there will be about the deep past. Both omnivory and scaffolding suggest that, not only are we likely to be wrong, but we are likely to be biased towards pessimism: we will expect less evidence than there will turn out to be. This is not a complete response to Turner (see Jeffares 2010) but it at least ought to give pessimists pause: betting against such resourceful methodology, particularly with reason to doubt your epistemic access to those resources, is a dangerous move.

Historical scientists live off the evidential equivalent of the smell of an oily rag. They prove remarkably resourceful in pushing their epistemic limits through a piecemeal, opportunistic methodology. Both methodological omnivory and evidential scaffolding suggest that we underestimate the epistemic resources available for uncovering the past. Pessimists, then, are likely to be biased in their assessment of historical evidence. In addition to this main point, I have also argued that due to evidential scaffolding some functional ascriptions in paleobiology ought to be read disjunctively, breaking the rule that we mustn't conflate causal-role and etiological function. Perhaps some epistemic rules were made to be broken.

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