
The Role of Analogy in Adaptive Explanation

By

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Abstract

Cases of ‘convergence’ (traits which have independently evolved in two or more lineages) could play an important role in the construction and corroboration of adaptive hypotheses. In particular, they could inform us about the evolutionary histories of novel traits. However, there is a problem of causal depth in the use of analogies. Natural Selection’s affect on phenotype is constrained by phylogenetic history to a degree that we are unfounded in projecting adaptive stories from one lineage to another. I will argue for two approaches to resolve this issue. First, by constraining our catchment area to closely related lineages we can control for developmental noise. Second, by integrating analogies into explanations which incorporate other streams of evidence or bootstrapping an analogous model across many instantiations, we can overcome the problem of causal depth.

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Introduction

In 1799 Dr George Shaw of the British Museum received a package from the naturalist Joseph Banks. The gentlemen of the Empire were collecting samples to catalogue the diverse flora and fauna of the realm. These were sent to Britain for scientific description and taxonomy. For the naturalists of the empire, Aristotle's 'Great Chain of Being' still held sway – the kingdom of life was divided into clear categories into which each member fell. They identified a Mammal, for instance, on specific criteria. A mammal is warm blooded, furred, feeds its young (who are born live), on milk and has separate chambers for excretion and reproduction. A Reptile, by contrast, has cold blood, thick scales, lays eggs and has a single chamber.

The contents of this package, a pelt, seemed to straddle several links in the Great Chain of Being. It was furry and warm-blooded like a mammal, but had a single hole 'down there' and laid eggs like a reptile. There were also avian features, webbed feet and a bill. Shaw was, at first, sure this was some kind of Antipodean prank.

The species in question, which (eventually) settled on the scientific name *Ornithorhynchus anatinus*, commonly the Platypus, caused such incredulity because of its similarities and divergences with other animals. If the platypus was a mammal, then why was it so similar to non-mammals? The suite of platypus traits tells us about something more than the species itself. It suggests that the links of the Great Chain are not as clearly delineated as first thought. Indeed, the platypus was one of inspirations for Natural Selection, which eventually laid Aristotelian theory to rest.

So the discovery of the platypus, and an examination of its similarities with other animals, tested Aristotelian theory. Because the theory assumed a strict delineation of groups, the platypus' failure to fit into these groups

counted as evidence against it. Conversely it counts as evidence for Darwinian Theory. Because evolution sees different lineages as phylogenetically continuous, we should expect to see border-line cases.

Analysing the similarities and divergences between animals can tell us many things; I am particularly interested in two uses. First is the testing of regularities and background theories, as we saw with the platypus. According to Aristotelian theory, the platypus cannot exist. Its discovery, then, falsified the old theory and corroborated an evolutionary perspective. Second, these resemblances or lack thereof can also tell us about the evolutionary relationships of lineages. For example, the traits of platypus mark it as a *Monotreme*. It is a mammal, but one only distantly related to placental and marsupial mammals. From this we can infer that a platypus shares a common ancestor with us in the more distant past than, say, a cow. Similarities between animals can tell us something about the evolutionary conditions required for traits to be selected. Platypus have webbed feet, much like a duck. A reasonable conjecture would be that both the duck and the platypus have webbed feet to help them swim.

This thesis is about similarities and divergences in animal traits and their inferential uses. In particular I want to know how we can use data from extant species to inform us about both extinct and other extant species. The similarities between us and the great apes, our closest relatives, base claims about the traits of our ancestors. We may think, for instance, that our ancestors lived in an arboreal environment in part because most of our relatives do.

Sometimes distant relatives can inform as well. Lineages living in similar environments tend to evolve similar phenotypes. This is commonly known as ‘convergence’. The stream-lined shapes of dolphins and sharks, the ‘counterparts’ of placental mammals that have evolved in marsupial lineages, and the evolution of flight in bats and birds are famous examples of this phenomenon.

What can we learn from convergence? Perhaps we gain epistemic access

to regularities about how Natural Selection moulds phenotype, how lineages are fit to niches, by reference to convergences. If we can understand these regularities, then they could provide a window into the evolutionary past of lineages which share those selective environments.

Many people who study the behaviour and cognition of animals, for instance, believe their work tells us not only about the particular animals they have examined, but about such regularities. Marino et al (2008) have compared the cognition and neural architecture of cetaceans and primates. The brains are divergent, but (they claim) cognition is convergent. This may show a decoupling of neural and cognitive evolution, suggesting that particular cognitive and behavioural traits will be selected for despite different neural histories and designs. Sayers and Lovejoy (2008) suggest that looking at social carnivores which "...hunt big game and cache meat, both of which approximate human hunting behaviour..." may be an inroad to regularities about the evolution of cooperative hunting. Plotnik et al (2006), upon discovering mirror-recognition in an elephant, had this to say. "Finding strong parallels among apes, dolphins and elephants in both the progression of behavioural stages and actual responses to a mirror provides compelling evidence for convergent cognitive evolution."

These scientists imply that the study of particular cases of cognitive evolution can help us develop a general theory. These general theories could then be applied to construct the evolutionary pasts of lineages we are interested in – our own, for instance. As we shall see, I'm not so sure this is the case, and will explore both my scepticism, and methods of allaying it, in the next seven chapters.

The first two chapters lay out the territory for the comparative work I am interested in. Similarities between lineages (or resemblance-relations as I sometimes call them) can be divided into two categories. Some are due to the inheritance of a particular developmental system which gives rise to particular phenotypes. These are homologies. Others – convergences – are caused by a continuity of niche, rather than inheritance. These are analogies.

So the traits of fur and warm-blood are homologous between platypus and other mammals – they have been inherited from a common ancestor. The webbed feet of ducks and platypus are analogous. They evolved independently from one another in response to the same selective environment.

I will argue for a particular conception of these terms. Homology and analogy are best understood as explanations of the phenomena of similarity. This sets me against some philosophers (particularly Paul Griffiths) who give homology special epistemic status. This discussion sets us up for the main concern of the thesis: the criticisms and eventual vindication of the use of analogy.

The third chapter introduces the problem of causal depth and develops a general language for its discussion. The problem of causal depth arises from the idea that some processes give worse ‘signals’ from the past than others. These processes may have left traces, but these are ambiguous as to their origin. Their reach from the past is ‘shallow’.

In the forth chapter, I claim that the use of analogies in inferences relies upon Adaptationism. Adaptationism has been rightly attacked in the last thirty years, especially by those philosophers and biologists interested in evolutionary developmental theory. I will show how taking these criticisms seriously undermines the epistemic worth of inferences relying on analogies. Natural Selection’s causal strength in forming phenotype is ‘shallow’ and so its ability to ground analogous inference is questionable.

The fifth chapter focuses our attention onto a particular inferential situation where analogous inference could be useful. These outlier lineages, as I shall call them, limit the utility of homology as a means of discovering the past because of phenotypic isolation. The hominid lineage, for example, is phenotypically isolated on two counts: It possesses a suite of traits unique among primates and all its closest relatives are extinct. Without homologies, comparative information from analogies would be welcome. I will also argue for a division of labour between analogy and homology in the

retrodiction of evolutionary histories.

The sixth chapter introduces the first solution to the problem of causal depth that I will consider, parallel-modelling. A defender of parallel-modelling claims that analogies only have epistemic warrant when used in highly developmentally constrained contexts. Because closely related lineages share similar developmental systems, there is a higher chance they will evolve similar adaptive responses to similar niches. By constraining our ‘catchment-area’, then, we can ensure that the environmental variables we are interested in are the factors which cause the evolution of our target trait.

The seventh chapter is about non-parallel analogies. I argue that although parallel modelling is a suitable approach given certain conditions, it is not the only solution to the problem of causal depth. Analogies can be valid when they are part of an integrated explanation. Analogous information can be part of the corroborating evidence for a hypothesis. The validity of these parts is taken as a whole rather than in isolation. I will also argue that several different analogues can be used to test and refine our model. Boot-strapping will both reaffirm our confidence in the regularity we are discovering and give us a firmer grip on the finer details of the evolution of the trait.

Finally, in the Coda I consider means of widening the explanatory framework I have laid down for analogies. I will claim that artificial physical structures (such as engineering and architecture) and design can occasionally be analogous to biological traits. If biological evolution is a special case of more general evolutionary processes, then perhaps we should expect to find something similar to homology and analogy in any selective regime. The argument is simple. If two lineages have analogous traits in virtue of those traits evolving through a similar selective process, then it is open to claim that any non-biological design which has ‘evolved’ through a similar process can also be counted as an analogy. Natural and artificial selection are different processes but, I think, they can be relevantly similar, and able to inform us about each other. The upshot of this argument is that the non-

existence of biological analogues is not an issue. We can, given the right conditions, make our own.

My aim in this thesis is to fill a gap. When philosophers and biologists examine the use of comparative data in biology, they typically focus on the use of homology and are disparaging about analogy. Those who have used and examined analogues have generally done so ignoring the criticisms which I shall rehearse. I argue that analogies can be successfully incorporated into evolutionary explanation. However, in order to use analogies we need a clear idea of which applications shed light on our past, and which do not.

1. Analogy and Homology

Before explaining the difficulties faced by analogous inferences, we need to know what the term means. As we shall see, analogy is defined in contrast to homology, so the next two chapters will give an account of both.

An analogy is an independently evolved similarity between two lineages. There are many documented cases of ‘convergent evolution’ – sharks and dolphins have similar streamlined design, bats and birds are both winged and in South America a marsupial (*Thylacosmilus*) evolved with striking similarity to the North American (placental) Sabre-toothed Tiger (*Smilodon*). These count as analogous because the common ancestor between the two species lacked the traits they have independently evolved (an extensive overview of cases of convergence can be found in Conway-Morris 2003).

Homology, then, is a similarity between two lineages which is present in the most recent ancestor. There are animals on earth which share the following properties: they give birth to live young who they feed on milk, they are warm blooded and tend to have fur or hair. We call these animals ‘mammals’ and they are similar because they share descent – the ancestor of all mammals also gave birth to live young, fed them milk, and so on¹.

This first pass at a definition of homology requires refining. It is presented as a definition, but is not quite an explanation. A trait being homologous between two lineages does not show that the similarity is *only* due to descent. Stabilizing selection may play an important role as without it traits may be lost. The degradation of eyesight in cave-dwelling lineages, for

¹ Or at least the ancestor of placental and marsupial mammals did.

example.

Analogy and homology are defined in relation to each other. Two similar traits are analogous if they are not homologous, and vice-versa. In order to discover whether a similarity is independently evolved, we must first work out the evolutionary relationships. We must test for homology and analogy². Typically definitions of analogy have been made in contrast to homology. If we can define homology then we have a definition of analogy in hand. Unfortunately, defining homology is not so straight-forward.

The definition from a biological dictionary demonstrates our difficulty. Two structures are analogous if “... their phyletic and/or developmental origin were independent of each other, i.e if there is homoplasy (Thain & Hickman 1996 pp26).” (As we shall see, tying our definition to ‘developmental origin’ is problematic due to both the decoupling of levels of homology and parallelisms). Homoplasy is a term from cladistics which we will take as interchangeable with analogy (for now). So, a definition of homology would provide a definition of analogy. However, Thain & Hickman’s first line says it all: “Homology. A controversial term (Ibid p311).” We need to grasp homology before we can make headway with analogy.

I will first give an overview of the concept of homology in the literature, consisting of three accounts. The *taxic* account defines homology in terms of the phyletic relationships between lineages. So warm-bloodedness is homologous between platypus and humans because the common ancestor of the two lineages was warm blooded. The *developmental* account ties homology to common developmental origins. So warm-bloodedness is homologous between platypus and humans because the lineages have relevantly similar developmental systems. The *transformative* account ties

² Paul Griffiths would disagree. He believes that homology must be tested for in order to show analogy, but not vice-versa. Why he thinks this, and why I disagree, will become clear through the chapter.

homology to relationships (‘transformations’) between particular traits. And so warm-bloodedness is homologous between platypus and humans because there are relevant similarities between the traits in the two lineages.

Following Griffiths, Brigandt, Love and others I accept pluralism about homology, whereby all three approaches are “...complementary aspects of an explanation of the phenomena (Griffiths 2007a pp 656).” Kim Sterelny (personal communication) has expressed that the transformational account collapses into the taxic account and, at best, ought to be seen as an epistemic criterion for recognizing taxic homology. I am tempted to agree (in my arguments in the next two chapters I will come very close to it) but as what I have to say for the remainder of the piece coheres with either conception I have opted to sit on the fence at least about that issue. My commitment to an account which gives analogy equal standing with homology will lead me to adopt a different account than that of other pluralists.

After the overview, I will describe Paul Griffiths’ account from *The Phenomena of Homology*. He emphasizes a particular approach (the transformational) to homology. Despite his pluralism, the transformational approach takes precedence.

This chapter sets us up for my own account, which I will describe and defend in the next. Though also pluralist, it contrasts with Griffiths’ account by taking homology as an explanation of biological similarity. Defending this view will involve a positive argument for taking analogy seriously.

The second chapter will close with a discussion on the relationship between function and physical description. I will use this to explore whether the identification of two traits as ‘the same’ is problematic. For now, I will assume that such identifications of similarity are robust.

1.1 A Survey of Accounts of Homology

There are three main accounts of homology in the literature. Before

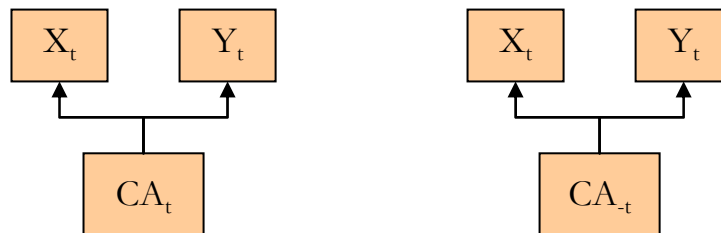
giving my account an overview of the current state of play is necessary. As pointed out in Brigandt & Griffiths 2007, the nature of the debate is similar to the species concept debate. We are not looking at definitions of homology so much as theoretical accounts, so they reflect different approaches to biological science as opposed to conflicting beliefs.

1.1.1 The Taxic Account

“... unity of type [fundamental structural similarity] is explained by unity of descent (Darwin pp240).”

According to the Taxic Account of homology, two traits are homologous if the trait was present in the ancestor of the two lineages in question. So a trait, t , held by two lineages, x and y , is homologous only if the common ancestor of x and y also had t . t would be analogous if the common ancestor of x and y did not hold t . To understand this, we need to look at some evolutionary fundamentals (I will provide a glossary for some of these terms at the close of the second chapter).

Figure i: Taxic Homology (synapomorphy) & Analogy (homoplasy)



On the left, the Common Ancestor (CA) of X and Y holds the trait (t), so the trait is homologous between X and Y. On the right, CA does not hold t , and so the trait is analogous

By evolutionary theory, life is a process of biological form (*phenotype*)

gradually changing over time. Phenotype is generally homeostatic between generations because similar, heritable developmental resources (the *genotype*³) are passed from parent to offspring. Many similarities between phenotypes, therefore, are due to the trait being present in a common ancestor – they are *synapomorphic*.

My father and I both have sandy-blond hair and grow red beards. In the parlance of systematics, we share the *character-states* of sandy-blond hair and red beards (at least when we do not shave). If we examine our family tree, we will find a fair few men with these same character states. Why would this be? They are synapomorphies – I have a tendency to grow a red beard because my father has the same tendency. If I had a red-bearded brother, the explanation for our similarity would be in terms of continuity of descent: we both have red beards because we share an ancestor with a red beard. So by the taxic account homologues are explained by descent. We do not just find continuity of character-states within lineages, but between them as well.

All primates form a *clade*, and in virtue of this share certain characteristics. A clade is a monophyletic group – it includes a single ancestor and all of her descendants (see Sober 1988 for a philosophically rigorous account). Some character-states, such as hairy bodies, five-fingered hands and forward-facing eyes are held in common between primates. By the taxic account, this is due to continuity of descent. Because of their common ancestry, all primates have similar genotypes and thus similar subsequent phenotypes.

The Taxic approach is utilized by modern systematics or cladistics. Character-states count as data points that are diagnostic of the evolutionary relationships between lineages. By quantifying the resemblance-relations

³ By 'genotype' here I do not refer to genes alone, the term here refers to whichever part of the developmental process is heritable, be it genetic, epi-genetic, cultural or environmental.

between lineages, systematists hope to trace how related they are. For a cladist, trait similarities between species are categorized as homologies or homoplasies. As we have seen, homology is due to descent. Homoplasy is simply a similarity, a shared character-state between lineages, which is not homologous. If they are independently evolved they are homoplasies. At this stage I will use ‘homoplasy’ and ‘analogy’ as interchangeable terms: by the taxic account, analogy is a similarity between character states which has evolved independently in two lineages.

Not all biological similarities can be categorized by the Taxic approach, however. As well as similarities between organisms, such as my beard and my father’s, there are similarities within organisms – *serial* homologies. My left and right arms share many character-states, as do my hands and feet (both have similar bone structure, five digits and are at the end of limbs). Each vertebra in the backbone is a separate individuated piece but they are all tokens of the same type. Because the taxic account examines character-states between organisms, it is blind to similarities within organisms.

The difference between analogy and homology is clear from a taxic standpoint. When a trait has evolved in two lineages independently, meaning that it was not present in their most recent common ancestor, then they are analogous (homoplastic).

1.1.2 The Developmental Account

The Developmental approach explains the mechanism by which homology arises in terms of the actual physical processes by which individual organisms develop. If the taxic account explains the congruence of character states between lineages, the developmental account explains the taxic account.

By the developmental account the similarity in beard shade between me, my father and my (hypothetical) brother is explained in terms of shared developmental information. We all utilise the same, or at least very similar, developmental resources – the same genotype. The genetic information which ‘codes’ for red shades in facial hair passed from my father to me. Our

phenotypic homology is due to an underlying developmental homology.

The developmental account unites serial and taxic homologues under one umbrella. My arms and legs are similar to one another, and similar to my father's arms and legs, because they are produced through the same developmental process⁴. An explanation of these similarities would involve an understanding of those processes.

It is important to make clear that merely being a similarity in developmental resources is not sufficient to qualify as a homology by this account. Homology and analogy can operate at different 'levels' of biological explanation. If two relevantly similar developmental systems evolve independently of each other, in principle this would be an analogy at the developmental level. Note that by the developmental account, if there is a developmental homology, there cannot be an analogy at the level of phenotype (see below).

We cannot define homology at the level of phenotype entirely in developmental terms, however (Griffiths 2007a). It is reasonable to believe that different levels of homology are decoupled (Brigandt & Griffiths 2007). You can have a homology in phenotype without a corresponding homology in genotype and vice-versa. Due to the amount of co-option and drift in developmental evolution, there are cases of phenotypic homology that are phylogenetically continuous but, over evolutionary time, now rely on different, non-homologous developmental resources. Nijhout (1985) has suggested this is the case for the development of wing patterns in butterflies. Some closely related butterflies have homologous wing patterns, but these patterns are caused by different, non-homologous developmental processes. We also see this decoupling in sex determination. The male/female dichotomy is presumably homologous amongst most vertebrates, but different mechanisms determine sex in different lineages. In

⁴ What counts as 'the same' developmental process is an open question I cannot explore here, although it is touched upon in my discussion of parallel evolution in chapter 6.

some cases (like our own), sex is determined largely genetically - activity during meiosis determines gender. However, in many other animals environmental factors such as temperature determine gender. Developmental homologues are used in phenotypic homoplasies as well. The *pax6* gene, for instance, is used in the development of the camera-like eyes of mammals and the compound eyes of insects – eyes which have evolved independently (Love 2007, Powell 2007, Gould 2002). It is homologous at a developmental level, but the eyes at the phenotypic level are not (see Raff 1996 pp 234-237 for examples from sea-urchin ontogeny). This means that we cannot reduce talk of phenotype homology to developmental homology.

The developmental approach is an important research area; it is required for a full understand of how homology and analogy evolve. A preliminary sketch is provided in both Griffiths 2007 and Brigandt 2007. The approach ought to be seen as complementary, not opposed to, the taxic conception.

The developmental approach will not be of much help to us here, however. If we lean too heavily on developmental resources we are unable to tell the difference between homology and *parallel* evolution.

Sometimes homoplasies evolve in closely related lineages using the same developmental resources, these are *parallelisms* (Powell 2007, Gould 2002, Diogo 2005). The concept will be extremely important later on, but here it will suffice to say that because parallelisms have evolved independently they count as data points for a different suite of inferences than if they were homologous. That homology and parallelisms have different inferential uses is good reason to preserve the distinction. No matter how close the evolutionary relationship between the two lineages, if the trait has evolved independently it has something to tell us about the conditions under which the trait evolves. If the traits are homologous, then they do not (although they may be able to tell us about selection's role in maintaining the trait over time). Because the lineages can utilize identical developmental resources in constructing phenotype, the developmental account cannot distinguish

between them.

1.1.3 The Transformational Account

“[homology is] The same organ in different animals under every variety of form and function (Owen, quoted in Brigandt & Griffiths pp 635).”

Before the acceptance of Darwin’s evolutionary theory, biologists categorized resemblance-relations between organisms using a set of operational criteria. This is the transformational account. The account is importantly related to the taxic (it is also used by cladists) but is different as it focuses on homology between particular traits, rather than the lineages as a whole. Homology here is not envisioned as “...a single, shared character state, but as a range of different states in which the same character can appear... (Griffiths 2007 pp648)” Consider milk-provision as homologous between humans and platypus. In most mammals milk is produced in mammary glands and expressed through specialized tissue (teats). In monotremes such as echidna and platypus milk is secreted through the skin. The echidna has two ‘milk patches’, whereas the platypus excretes the milk, sweat-like, from its skin. By the transformational account, human and echidna milk provision are homologous because they are variations on the same character. We can see a transformation from the platypus’ general excretion, to the echidna’s patches, to the placental mammal’s teats.

To understand the difference between the taxic and transformational accounts, we must articulate the difference between a *character* and a *character-state*. The taxic account infers homology based on character-states. These are (typically) binary states that a trait may occupy in a particular lineage. I either have a red beard, or I do not. A character, which the transformational account focuses on, considers traits at a coarser grain. Red beards and black beards are both variations of the character ‘beard’.

By the transformational account traits which are homologous are, in some sense, the same trait. Owen defines homologies as being the same organ under every variety of form and function. To say traits have phylogenetic continuity is to say they are tokens of the same type. The

swim bladder is a kind of modified lung which is used in ray-finned fish to control buoyancy by increasing and decreasing gas⁵. This is not its only function, however: in some fish it is still primarily used for breathing and in others it has been co-opted for use in hearing (Dawkins 2004). By the transformative account, focusing on the character, the lung and the swim-bladder are homologous. They represent transformations of the same morphological structure. A taxic account focusing on character-states may see the swim-bladder and a lung as non-homologous as they are diagnostic of a split between the two lineages. When compared to a different lineage which lacks swim bladders or lungs altogether, however, the taxic account may see them as homologous as they will unite the groups into a clade, with the new lineage as an outlier.

The criteria by which homology is set by this account are as follows:

Traits can be similar *topographically*. Their resemblance-relation may be in terms of position, size and structure. The eyes of primates are homologous because they are all forward-facing; occupy the same space in the skull; are a similar size and so on. It is in virtue of their similarity in organization that we recognise their homology.

Alternatively traits could be similar due to *special qualities* – “... shared features which cannot be explained by the role of a part in the life of an organism (Griffiths 2007, pp 658).” These special qualities are arbitrary, such as the position of the blood supply to the retina in the vertebrate eye (Griffiths’ example). Some bird species do complex and ornate dances as part of their mating routine (Love 2007). There is no particular functional reason for them to dance as such (other birds seem to breed perfectly well without dancing) so it is unlikely that it evolved independently in the lineages. The characters can also unite clades. All spiders have spinnerets,

⁵ As surprising as it may seem, it looks like lungs evolved first. The ancestral lung evolved into the swim-bladders of ray-finned fish and the lungs of terrestrial mammals. See Dawkins 2004’s discussion and Farmer 1997 (she argues that the ancestral ‘lung’ was for oxygenating the heart).

organs usually located on the abdomen which produce silk. Having this organ (or at least the vestige of it) is considered both necessary and sufficient for entrance to the spider clade.

Finally, homology can be recognised in terms of intermittent forms, or *transformations*. The feet of Homo-sapiens and other primates can be seen as variations upon a particular structural theme (Chapais 2008, chapter 1). The skull-shapes of vertebrates are all versions of the same basic design. The skull might be elongated for a horse, flattened for a crocodile or expanded for an elephant. It might have different kinds of horns, antlers and other bells and whistles. Overall, however, the skulls of all vertebrates are elaborations on the same character. For the systematist, this could act as a data-point for clade construction.

However, the status of analogy in the transformational account is unclear. By using these three criteria, biologists can determine whether particular characters are homologous or not, but what would it mean for a trait to be analogous? Analogy cannot mean dissimilar – it is independently derived similarity. Perhaps if the characters are not similar enough to each other they may count, but to what degree? Because the transformational account looks at homologous relationships between particular traits, it is not clear how it can identify analogy.

I will take a paradigm example of analogy, the evolution of similar body shapes in sharks and dolphins, and see what the transformational account will make of them. By the transformational account shark and dolphin body design could be seen as homologous – they are both transformations of the basic vertebrate body structure.

Alternatively, they could not be homologous. Consider the transformations of the tail and backbone in the two lineages. Sharks have retained the backbone structure of their aquatic ancestors and so swim along a vertical axis. The cetaceans, by contrast, have been originally adapted for terrestrial motion and so swim along a horizontal axis, ‘galloping’ through the sea. So the shark is a transformation of the fish

body shape and the dolphin a transformation of the terrestrial mammal body shape (both of which are sub-sets of the vertebrate body shape). These two different characters both share a similarity in the method in which they generate forward motion in an aquatic environment: they flex their backbone to swing their ‘tail’. We could perhaps view this as an analogy – two different characters have evolved similarities.

There are three problems with this attempt to define analogy in transformational terms. First, it is not clear that the move is independent from the phyletic relationships between the two lineages. To see the body shapes as independently evolved, we need an evolutionary history of the lineages in question – and this is a taxic conception. So in order for the transformative account to give us analogy, it must collapse into, or at least work in partnership with, the taxic account.

Second, whether the transformational account should view shark and dolphin body-design as different characters is up for debate. Analysing them as homologies is more aligned with the concept. It is clear that both are transformations of similar designs – their resemblances outweigh their differences (particularly when compared with invertebrates).

Third, this story radically limits what can count as an analogy by tying it to similarities in different characters. If a similarity is within the same character, this could not be analogous. This would discount parallel evolution. Perhaps the similarities between mammal and cephalopod eyes could count as analogous, because there is not a transformative chain that links them. However, given the similarities between the two characters I would argue that claiming a lack of transformative chain presupposes knowledge of the evolutionary history of the two lineages – again, it is reliant on the taxic conception.

This is important for future discussion: **the transformational account cannot define analogy** – at least without collapsing into the taxic account. If we are to envision the transformational account as independent, and in fact as having priority, over the taxic (which Griffiths does), then analogy

falls out of the picture.

Griffiths has argued that the transformational account is an ‘experimental tradition’ and homology should be viewed as a pre-theoretic phenomena (pre-theoretic to an overarching ‘theory’ at any rate). This argument has important consequences for my position, so I will take some time explaining it.

1.2 Is Homology Pre-theoretic?

In Paul Griffiths’ 2007 paper *The Phenomena of Homology* he argues that homologies in the transformational sense are “... robust descriptive phenomena (pp655).” This argument is important because it explains some of the reason that analogy may be in disrepute, and defusing it will give an impetus for my account. Griffiths’ position is best seen as consisting of two claims. One I agree with. The other I do not, and will dispute.

Griffiths argues that homology is a ‘mind-independent’, non-gerrymandered phenomena— it is *pre-theoretic*. A phenomenon pre-theoretic if it is not postulated in light of an overarching theory. Some of the postulates of quantum mechanics, for instance, may not be pre-theoretic. Currently unobserved particles which are postulated to explain observations may be reliant on theory. Our commitment to the existence of these phenomena is dependant on the confirmation of the theory and its postulates. For some postulates in physics, the jury is currently out. Pre-theoretic phenomena, by contrast, require explanation even if the current paradigm is false. When Ptolemaic Astronomy was rejected the sun’s apparent movement across the sky was still a phenomena which a new theory had to account for. “...[H]omologies are robust phenomenon that stand in need of explanation and whose reality is to some extent independent of current theory (Ibid, pp651).”

Griffiths does not only argue that homology is mind-independent. Homology for him is in some sense a fundamental phenomenon – the transformational criteria do not infer homology, they recognise, or diagnose it. The taxic account is merely an explanation of homology, not truly a

definition. This affects my aim of giving an account of analogy because it puts analogy on a lower epistemological footing than homology. We recognise homology, but analogy must be inferred – there is an epistemic asymmetry between them.

‘Pre-theoretic’ does not mean empty of all theory, but independent of an overriding theory⁶. The transformational account does contain ‘theory’ in the broad sense. The three criteria for identification could be seen as theory. However, Griffiths argues that these criteria can stand alone independent of a unifying theory of the kind usually referred to by philosophers of science. Griffiths bases his position on the New Experimentalists of the 1980s.

For the New Experimentalists, the theoretical and experimental (or observational) aspects of scientific work can be decoupled. The most well-known example of this is Ian Hacking’s work on microscopy (Hacking 1981). When microscopes were constructed, the experimental work that proceeded did not test any particular theory, but collated data. The existence of Microscopic phenomena can be argued for independently of microscopic theory. A macroscopic phenomenon may be shrunk and then viewed through the microscope to ensure they are similar. As Griffiths puts it, “These arguments for believing what is seen through a microscope do not appeal either to the kinds of theories we use microscopes to test or to the theory of the working of the microscope. Instead, they provide direct, independent, reasons to accept the reality of the phenomena observed with the microscope (Griffiths 2007 pp 652).”

Griffiths replaces the direct testing used in the microscope case with an argument from success based on the work of the pre-Darwinian

⁶ ‘Pre-theoretic’ is, perhaps, the wrong term. There is a difference between the ‘pre-theoretic’ nature of our observation that the sun crosses the sky during the day and homology. Another way of reading my arguments in the next two chapters is in claiming that *resemblance-relations* are pre-theoretic (in a similar sense to the sun’s path), whereas homology and analogy are explanations of it.

Anatomists. He cites uses of the comparative method which correctly resolved disputes around homology (such as the relationship between human urinary-genital system in embryo and adult). That this was the correct analysis, as later confirmed under the aegis of Darwinian theory, provides evidence that the phenomena is pre-theoretic. “A history of success in using these predicates in a wide range of inductive inferences provides grounds for supposing that they taxonomise the phenomena in a way that corresponds to actual causal processes in nature (Ibid pp 653).” So because the anatomists were successful in their diagnoses of homology despite lacking an overriding theory, we should believe that homology is mind-independent.

The New Experimentalists claimed that an experimental tradition may accumulate knowledge independently of theory, and Griffiths claims this for pre-Darwinian uses of homology. The failure of the theory of Ptolemaic Astronomy does not falsify the observations of heavenly bodies that were made in the fifteen hundred years before Copernicus. When Copernican theory gained credence, it did so on the basis of providing an explanation of data garnered earlier. Working without an overriding theory like Evolution, the anatomists nonetheless provided much of the evidence for Darwin’s theory. This shows that the observations and data collated was independent of that theory, they preceded it. The anatomists were not making an inference when they diagnosed homology; they were recognising an overt phenomenon.

I do not believe that the distinction between inference and recognition is sharp. There are border-line cases (if, for example, folk psychology turns out to be radically false as Paul and Patricia Churchland have argued, do categories such as ‘belief’ and ‘desire’ still require explanation?). This does not overly affect Griffiths’ thesis, however. He just needs to claim that homology is significantly more robust than analogy.

However, I do not think we ought to be convinced of Griffiths’ argument from success. Consider another area where pre-Darwinians have

been very successful: species identification. In the introduction I made a passing reference to the Great Chain of Being which the platypus' discovery upset. We may notice how successful these Aristotelian taxonomies were – generally pre-Darwinian naturalists got it right. Counter-examples such as the identification of the barnacle goose and barnacles as the same species notwithstanding, typically species were correctly identified despite lacking any evolutionary theory. Moreover, as Diamond & Bishop (1999) have demonstrated, folk conceptions of the divisions in nature are remarkably astute. Does this success mean that we ought to privilege a pre-Darwinian conception of species? It is hard to see why. This success does support the claim that the category 'species' is in some sense mind-independent – they are phenomena in need of explanation by whichever theoretical framework we employ. But we do not think that a folk definition of 'species' is somehow epistemically fundamental.

So Griffiths has argued for homology being a mind-independent, pre-theoretic phenomenon. I agree. He also claims that homology is, somehow, fundamental – it is the non-inferred target of some evolutionary explanation. I do not think his argument is enough to support his second claim, but as the discussion falls on the relative merits of the positions qua their explanatory potency, I want to go further and present reasons why we should be unhappy with Griffiths' account.

An important implication of Griffiths' position is the epistemic asymmetry between homology and analogy (made explicit in Griffiths 2007b). If homology is simply recognised, but analogy can only be inferred, then we should believe that homology is less epistemically demanding than analogy. We need to rule out homology before we can consider analogy. To support an adaptive claim about the emergence of a trait, we may wish to point to an analogous example. For instance, that dolphins, sharks and ichthyosaurs all evolved similar streamlined shapes is good evidence that there is selective pressure towards that body-shape. However, to count as data-points for the inference, the examples must be independently evolved. As Griffiths correctly points out, it is the instances of independent

evolution that count, not merely any instance of the trait. If the traits are homologous, then Natural Selection has no part in explaining the trait's emergence (although it may be important in maintaining homeostasis through time, see Griffiths 1994).

Why should I be concerned with epistemic asymmetry? We can still identify analogies, albeit in a secondary step, and use them in inferences. There are three reasons. First, in 2007b Griffiths uses the asymmetry to claim that homology ought to be preferred in evolutionary explanation (as it is less epistemically demanding). Second, it is very hard to understand how it could be that we need to identify homologies in order to use analogies, but not vice-versa. The third, and main, reason is that I think the asymmetry simply does not exist – it does not exist because homology is no more fundamental a phenomena than analogy.

Before moving to my arguments, it is important to point out that there is a sense in which we can read the epistemic asymmetry between homology and analogy without requiring Griffiths' second claim. To explain this, we need to finally distinguish between homoplasy and analogy. A homoplasy is a case of independently evolved similarity - how we have up until now defined analogy. An analogy is a case of independently evolved similarity which has evolved due to the same selective process. Perhaps the webbing on ducks' feet evolved in order to swim more efficiently but the webbing on a platypus evolved for some other purpose (perhaps an ancestor used to glide between coolibah trees). If this was the case, then there would be homoplasy between the two lineages, but the traits would not be analogies.

So, it is one thing to claim that a resemblance is homoplastic, but another to claim it is analogous. To make a claim of analogy, we must first control for homology by drawing our clades and confirming homoplasy. We then need to show that the homoplasies are due to the same selective processes. We want to shift from a mere definition of analogy, to analogy as an explanation. For analogies continuity of niche explains the resemblances. For mere homoplasies, continuity of niche does not explain them. We do

learn something about selection from this – that the traits are open to being selected (at least in those lineages), but this is relatively uninteresting.

So, if this line of thought is right, there is no epistemic asymmetry between homology and homoplasy, but there is between homology and analogy. In the case of homology we control for homoplasy by cladistic analysis. In the case of analogy we first control for homology by cladistic analysis, and then confirm that the two lineages have relevantly similar selective environments. This means that analogous similarities are such on two counts: they are similarity in character as well as similarity in selective environment.

I think this version of the asymmetry is misconceived because a parallel argument can be run against homology. Let us imagine two different cases of homology. In the first, the explanation of homology is simply descent. Perhaps the warm-blood of mammals has been retained across evolutionary time because that trait has become entrenched in the mammalian developmental system. In the second, descent is not the whole explanation. Maybe warm-bloodedness is actually extremely labile developmentally, perhaps some environmental factor (such as temperature) had a strong influence, or the genetic correlates themselves were particularly prone to mutation. If that was the case, then the reason that mammals are warm-blooded is not simply that it was inherited, but that any mammal born without a way of internally regulating their temperature is selected out of the population. In the first case, descent plays a large role in explaining the similarity. In the second case, stabilizing selection plays a large role.

So, if we expect homology to be an explanation of the similarity, we need to control for stabilizing selection. This is to divide the cladist's term synapomorphy from homology. It is one thing to say a trait is synapomorphic in two lineages (it is held by the common ancestor), it is another to say they are homologous (it is held because it has been inherited). This, like in the analogy case, would constitute a second step in the identification of a homology. There is no asymmetry here unless we,

like Griffiths, think that homology is somehow more fundamental than analogy.

The next section will give reasons to disagree with the claim that homology is a fundamental, non-inferred phenomenon. This will prepare us for my account in the next chapter.

1.3 Fitting Analogy into the Picture

My purpose is to discuss analogy, so the approach to homology I take must be amenable to it⁷. As we saw in the last section, accepting pluralism about accounts of homology does not necessarily put analogy and homology on equal footing. An account of analogy is only clearly given by the taxic account and, if we accept Griffiths' arguments, the taxic account is of secondary importance to the transformational (because the transformational account diagnoses the phenomena of homology, whereas the taxic only explains it). This puts analogy on the backfoot before we even have a chance to discuss its epistemic status.

This section will present two objections to Griffiths' account, which I hope are extendable to any definition of homology which gives the transformational approach priority. The first objection relies on the transformational approach's inability to discern between parallel evolution and homology. The second claims that there is a tension in his account.

If we agree there is an important difference between cases of parallel evolution and homology, then the transformational account must be inferential. Why? Because cases of parallel evolution can be as similar, by transformational criteria, as cases of homology. Merely examining the character-similarity does not tell us whether they are homologous or analogous. Very close similarity provides strong evidence for homology, but

⁷ One option which I suppose is open would be to take a pragmatic stance in relation to this issue. Just taking the taxic account would make this job simpler. I do think that it can be justified on stronger grounds than pragmatism, however.

does not guarantee it. Only the holistic approach given by the taxic account, which uses a suite of different character-states to set the relationship between organisms, can distinguish between homology and parallel evolution.

This does not make homology mind-dependant, but it does mean we should reject Griffiths' second claim – that homology is in some sense fundamental; that it is observed, not inferred. In response Griffiths could claim that our inability to observe something with certainty does not mean that the phenomenon is not in fact observed. I agree, but if we want to preserve the distinction between parallel evolution and homology then it cannot be the case that the transformational account picks out homology as a fundamental, non-inferred category.

I can now move onto the second argument.

This objection to Griffiths' position is fairly complex. An intuitive version goes as follows. For Griffiths, analogy is epistemically parasitic on homology because homology is a robust, pre-theoretical descriptive phenomenon. But analogy is pre-theoretical as well. What is more it is recognised the same way as homology (see below). If this is the case then there is a tension between the nature of analogy and Griffiths' account of homology. All else being equal, if we can find a theory which resolves this tension it ought to be preferred. Here it is in more formal terms.

1. Griffiths' First Claim: homology is pre-theoretic
2. Griffiths' Second Claim: homology is a 'fundamental' phenomenon which is not inferred
3. By Griffiths' account, the taxic approach provides an evolutionary explanation of homology (not a definition) (due to 2)
4. The transformational approach cannot provide an account of analogy (only the taxic can)
5. Analogy is epistemologically secondary to homology (from 2, 3 & 4)
6. Analogy is pre-theoretic

7. Analogy and homology are both ‘pre-theoretic’, descriptive phenomena which are recognised through very similar, sometimes the same, methods (from 1 & 6)

8. There is a strong tension between 5 & 7

The argument does not show that Griffiths is wrong, but instead motivates my account which will resolve the tension between premises 5 and 7 by denying premise 2. The two key premises I need to argue for are 4 and 6. I have already argued for 4, but 6 will require more work.

As we have seen, Griffiths’ argument for taking homology as pre-theoretic is founded on two points. The first is an argument from success. Because the anatomists were largely correct in their predications of homology, we ought to believe that they were describing a robust phenomenon. The second shows that homology’s recognition is independent from the theory which explains it. What could provide similar arguments for analogy?

There does not appear to be an argument from success for analogy, or at least it is beyond the scope of this project. Most of the work undertaken in evolutionary biology which could use analogy has either been informal theory corroboration which has not been clearly successful (Gould & Lewontin 1979, Griffiths 1994) or formal population biology which has typically been too abstract to make use of real-world exemplars. As we shall see in chapter 4, there may be reason to think that analogy has been particularly unsuccessful, or at least it is very difficult to ascertain what its success would look like⁸. Having said this, the example of Cuvier against Owen is telling. Cuvier emphasized functional continuity in his pre-Darwinian anatomy and was at least as successful as Owen. I will argue that analogy is a descriptive phenomenon based on an argument for theoretical

⁸ One case that certainly looks like success to me is the predicted life-way of a eusocial mammal based on insect analogues which was confirmed in the discovery of the naked mole-rat (Dawkins 1976).

independence.

1.3.1 The Phenomena of Analogy

This section will present reasons for agreeing with premise 6 of my argument above: that analogy, like homology, is pre-theoretical – it precedes evolutionary theory. I will argue that the means of identifying function in artefacts and biology, functional analysis, is independent of evolutionary theory. If this is the case, then independently evolved resemblance-relations in biology (analogies), functional similarities, are also independent of evolutionary theory (at least epistemically – they, like homology, clearly need evolutionary theory for explanation).

How may we infer, from a physical description of an artefact, what its function might be? For any given function, there is a range of ways it may be actualized. This means that for any given structure, there are only so many functions which that structure might be an instantiation of. As Kroes (2006) puts it, “From the structural description of a spoon I may easily conclude that that object is not a copying machine, and from the functional description of a spoon, I can reasonably infer that the Empire State Building is not a spoon (pp 143).”

Daniel Dennett (1995) has argued that the more complex an artefact, the more likely it is that we can identify its function. As complexity in physical structure increases, the range of possible functions that structure might instantiate decreases. To borrow Sterelny (2003)’s example, we can be confident that a three-pronged spear is for fishing as opposed to hunting because its design features make it efficient for spearing fish but, due to its light weight, useless for hunting terrestrial animals.

So, for very complex artefacts, purpose becomes less ambiguous. Recall Paley’s 19th Century version of the argument from design (Paley 2006 (1803)). He asks us to imagine discovering a watch in a location not typically visited by humans. It is suggested that we deduce that, due to the clear design of the watch, there must have been a designer of it. Ignoring this teleological move, let’s ask instead why we call this object a ‘watch’ in the

first place. If we are to design a working watch using clockwork, there are very specific constraints on our design. The clockwork must be regular enough to keep time, it must relate in the right way to the clock face to be able to represent time, and so on. Due to this, only so many options will work, and it would be surprising if something meets the functional criteria of being a watch, but is not. I will now move to a biological example.

‘Wing’ is clearly a functional, as opposed to phylogenetic term. The wings of bats, birds and insects (not to mention aircraft) are not homologous (although bats and birds use some homologous structures), but we are happy to identify them all as wings due to a continuity of purpose. So, if a structure’s function is unidentified – if we have not seen it ‘working’, upon what basis could we claim it is a wing?



Figure ii: Bellerophon Mounted on a Pegasus, Peircing the Chimera

There are massive constraints on what will create a working wing. The requirements depend on the mass and shape of the object to be lifted, the physics of the environment itself and the available materials. Attaching a pair of swan’s wings to a horse, as in Reuben’s 1635 painting (*Bellerophon Mounted on a Pegasus, Piercing the Chimera*), would not provide the intended result. If the horse somehow managed to get off the ground, it would not remain above it

for long. The engineering constraints of flight restrict what counts as a working wing in the same fashion that watches are restricted.

The upshot of these engineering constraints is that certain functional ascriptions can be made merely on recognition of those constraints, and this is as true for designed objects like watches as it is for ‘design-like’ biological objects like wings.

When we recognise an analogy in biology, we do this on the basis of

resemblance-relations which in some cases would also be picked out by the transformational account. In the case of a wing, we recognise topographic similarities in the organization of, say, a bat wing and a bird wing. Their make-up is very different in important respects, but they still have continuity of form due to the engineering constraints required of them. The similarities between dolphins and sharks can also be put in topographical terms: 'stream-lined' implies functional use, but is recognised in terms of form. As pointed out earlier, in the case of parallel evolution the similarities are closer and in some cases are indistinguishable from homologies based on transformational methods (a fuller account of the relationship between function and form will be given in the next chapter).

So, when there is striking similarity between disparate lineages we can sometimes refer to engineering constraints (such as aerodynamics) to describe that similarity. No-one denies this, but essential for my purpose is what follows: these 'design constraints' are pre-theoretical. They do not rely on an overarching theory of biological form. They are a description of the phenomenon, albeit a thick, theoretically informal description, as well as part of its explanation. In short, we should agree with premise 6 of my argument.

If 6 is the case, then the tension in Griffiths' account becomes apparent. Griffiths undermines analogy by making homology as described by the transformational account a robust, descriptive phenomenon which is in some sense fundamental: the explanatory target of the taxic account is homology itself. Analogy is then epistemically parasitic on homology and is inferred using methods reliant on Darwinian Theory (the taxic account). But analogy is also a descriptive phenomenon to be explained and in some cases (particularly parallel) is recognised by the same criteria as homology is. How I think this tension ought to be resolved is the topic of the next chapter.

2. Analogy and Homology as Explanations of Biological Resemblance-Relations

This chapter will explain my account of homology and analogy. It will be linked to a general story about the explanation of similarity. The best account of homology conceptualizes both homology and analogy as possible explanations for character-congruence. The level of similarity is fixed by the transformational method, and in combination with the taxic approach we infer which explanation is most likely.

The first two sections will present my account of homology and analogy. I will argue that we should not view the transformational method as a non-inferential way of diagnosing homology, but instead an operational criterion for recognising resemblance-relations between characters. Homology and Analogy are then conceived as inferred explanations of character congruence⁹.

My account is deliberately vague on what will constitute a similarity. As we shall see, I think that all resemblances, not simply the most obvious, may be placed into three categories: this is my task in 2.1. Moreover, although I tend to use morphological examples for ease of exposition I hope (and intend) that, with minimal changes, my account can be applied to similarities at the molecular, behavioural and cognitive levels.

I give three reasons to prefer my account (at least over Griffiths'). First, in the last chapter I argued that the transformational account's inability to

⁹ This is similar to the account given in Coates 1993 insofar as the 'conjectural' nature of homology is emphasized. "Any conjecture of homology is therefore equivalent to the cladists' synapomorphy, and consequently remains transformable into an instance of convergence or parallelism (homoplasy) by the introduction of new data into the classification. (pp412)

discern homology from parallel evolution suggests that homology is inferred. I also argued in the last chapter for a tension in Griffiths' account, the second reason will be that my account relieves that tension. Third I will show how my account coheres with a general account of similarity explanation.

In the last chapter I concluded that Griffiths' account has a tension arising from his claim that homology is a non-inferred description and my claim that analogy is pre-theoretic. I resolve this tension by denying Griffiths' claim that homology is non-inferred (2 in the formal version). Homology is not recognised using transformational methods, biological resemblance-relations are. If we take the transformational method as describing resemblance-relations and homology and analogy are taken as inferred, evolutionary explanations of these relations, then the problem will dissolve.

By my account, the fundamental phenomena, the explanatory target, are resemblance-relations between and within biological objects. Animal Design-Space is not a phenotypic free-for-all. In the scope all of possible forms, nature is surprisingly conservative. Comparisons between empirical morphospaces (which plot measurements based on data collated from actual animals) and theoretical morphospaces (which plot "... hypothetical yet potentially existent morphologies" (McGhee 1999 pp15)) have shown that of the amount of theoretically possible forms out there, very few are actualized. Morphology tends to cluster; morphospace is 'lumpy'. Although a theoretical morphospace may not be independent of evolutionary theory, empirical morphospaces are - they are simply the measurement and categorization of traits. Resemblance relations, then, are striking phenomena independent of any particular overriding theory.

One advantage of taking resemblance-relations as the fundamental phenomena is that it allows explanation of biological resemblance to fit in with a more general account of similarity-explanation. Due to its reliance on the transformational method Griffiths' account cannot do this.

2.1 Sketch of a General Account of Similarity Explanation

Similarity, when it occurs, is due to some combination of three explanations. The similarity may be due to continuity of origin, continuity of process, or accident. In biological terms, analogy relates to continuity of process and homology to continuity of origin.

With many surprising cases of similarity we might apply what Sober refers to as the principle of common cause (Sober 1988). When we discover a similarity between two objects, an explanation which postulates the same cause for both is preferable. Why we should prefer this will be briefly touched upon in the context of cladistic parsimony in the next chapter. Here I just want to point out that both continuity of origin and of process both fit within this principle. Accidental similarity does not.

We may hypothesise that similarity is due to a *continuity of origin* – they come from the same source. Two cars may be similar due to being manufactured according to the same assembly instructions, or at the same factory. Chocolates of the same type will resemble one another due to being constructed from the same materials, using the same recipe and coming from the same mould.

Sometimes similarities arise independently of each other, and this may be due to a *continuity of process*; perhaps a purposive ‘selective’ process, or a mechanical process. All igneous rock is formed by the process of magma cooling, and rocks will resemble each other in virtue of this. Artefacts built with similar purposes may have resemblance-relations due to being affected by similar selective processes. The design of a traditional Maori Pa resembles a medieval castle. Both are built on high ground where possible, have high walls, look-out towers and so on. These resemblance-relations existed because the requirements of the kind of warfare the two societies engaged in were the same.

Some independent similarities may be due to *accident*. It is not merely chance, as there may be good reasons for the similarities, but if they are

different reasons, then their similarity counts as accidental. Not much can be made of accidental similarity. However, the more striking the similarity or the more obvious the cause of the similarity, the less likely accident is the explanation. That birds and aeroplanes share characters is surely not an accident.

These explanations are not mutually exclusive, and often the best account of a resemblance-relation will draw upon all three. Two roman arches will share distinctive characters. They will be semi-circular, have an odd number of slightly wedged-shaped stones (voussoirs) and require a great weight of masonry on either side to avoid bulging. These resemblance-relations are in part due to continuity of origin. Roman architects made up for a lack of theoretical understanding by adopting strict formalism – there was a particular way that one built an arch and this is reflected in the similarity between arches from this period. They also used the same materials wherever possible. This alone does not account for the similarity, however. The arches are subject to the same physical processes and their design reflects their purpose. By converting a vertical load into a lateral one distributed across the voussoirs an arch is able to support great weights (Gordon pp 187-189). If the arch design varies too much the weight could be unevenly distributed and it could collapse. Perhaps some of the resemblances between any two arches are accidental as well. Perhaps the rock that was used happened to have stratified into the same pattern. I want to look at one more non-biological (and light-hearted) example before returning to the fold.

Erich von Daniken hypothesizes continuity of origin to explain character congruence between the pyramids of ancient Egypt and the Central American Mayans. “They [particular pyramids in the Americas] have the same pyramidal shapes as those in Egypt. Who copied from whom?... Could it be that all pyramids everywhere in the world had the same master-builders? (von Danikan pp 33-34, italics removed)” Continuity of origin is an extremely implausible explanation for the phenomenon of pyramid building in South America and Egypt. How could there have been contact

between two peoples separated by great distances, both spatial and temporal? There is very little archaeological evidence to suggest any such meeting. Including aliens into the mix, as von Danikan is wont to do, does not help the plausibility of the hypothesis.

Fortunately, congruence due to similarity in selective process, as in the castle-Pa example above, seems very plausible indeed. When desiring to construct a large building using heavy stone the structure of a pyramid is ideal. In addition to being very strong structurally (the weight is evenly distributed around the base), it is also pragmatic in construction: piling similarly shaped stone bricks on top of one another will create this effect.

Accident should also be taken into account. Considering the breadth of possible examples for von Danikan to pick from (all buildings made by all ancient peoples) it is a little remarkable that he is only able to point to similarities between two particular cultures. When looking for similarities – particularly for the purpose of testing generalizations – we must avoid ‘cherry-picking’ our examples (a problem we will discuss in more detail for biology in the next chapter).

The amount of congruence lends credence to a continuity of origin hypothesis. If two sets of pyramids were similar in terms of special features (if both had sphinx, for instance) or in terms of transformations (if we could see a clear development of style between them) then it would give us pause. Features as arbitrary as sphinx or specific as stylistic continuity are very unlikely to be due to common engineering features (the justification for thinking that character congruence provides good inferential grounds for phylogenetic claims is a main focus of Sober 1988, and discussed in chapter 3).

Griffiths’ account does not fit with this general story about similarity selection. As opposed to just recognising a similarity, which is then explained in terms of continuity of origin (descent, homology), process (niche continuity, analogy) or accident, when we describe continuity of origin in a biological context a different set of rules apply. We somehow

immediately recognise the similarity as homologous with (at most) minimal inferential considerations. This does not seem to be the case, particularly taking parallel evolution into account – a glance at the debates in systematics shows that we are frequently wrong in our initial diagnoses of homology. Seen in this light, Griffiths’ arguments for homology being ‘fundamental’ are not enough to support his claim.

With my account in hand, then, I want to turn to a case study from systematics and see how this can be read in light of it.

2.2 Similarity in Biology

I will look at Hans-Peter Schultze’s 1994 work contrasting seven competing hypotheses on the phylogenies of sarcopterygian fishes (Schultze 1994). The sarcopterygian, or lobe-finned, fishes are of special interest because of their relationship to tetrapods. Tetrapods evolved onto the land and gave rise to the amphibians, reptiles, birds and mammals in the late Devonian. It is supposed that the limbs of land animals evolved from their bony protruding fins. A central question is whether the tetrapod lineage is more closely related to extant sarcopterygian lineages (lungfish for example) or to extinct ones (see Coates 1993 for a philosophical review).

Examining a series of cladistic studies, Schultze compares two evolutionary hypotheses. In the first a clade is formed by the extinct lobe-finned fishes and tetrapods, extant lobe-fins being an out-group. In the second the extant lobe-fins and tetrapods form the clade.

Figure iii Hypothesis One

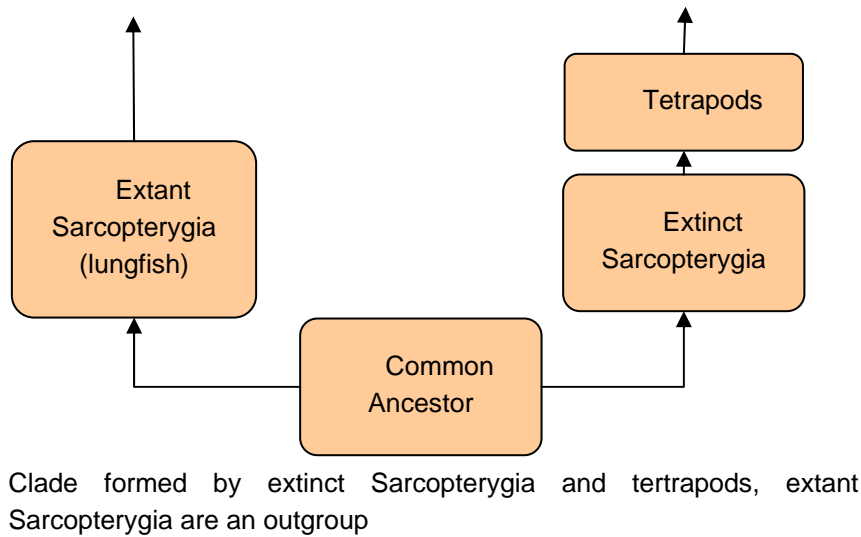
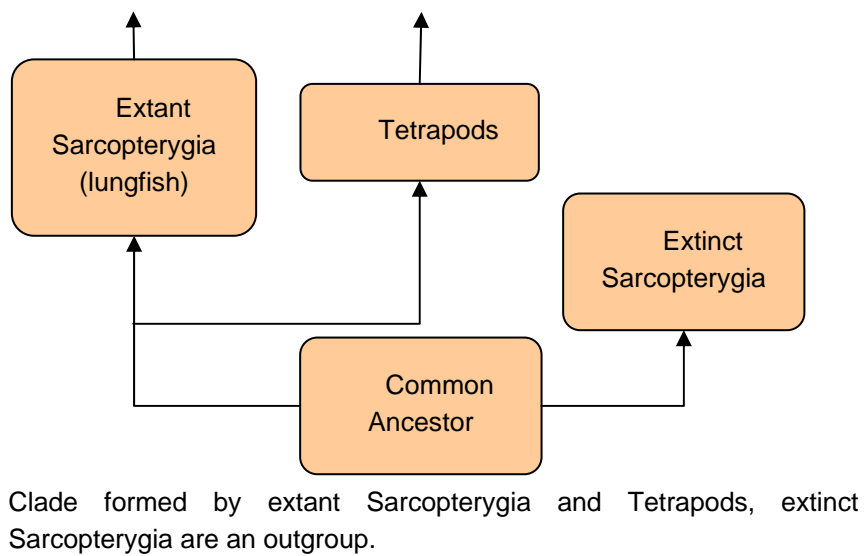


Figure iv Hypothesis Two



There is a proposed homology which Schultze rejects, and his reasons for doing so are revealing.

One of the proposed homologies between a sarcopterygian lineage, the

dipnoans (lungfish) and tetrapods is between the posterior internal nasal opening in dipnoans and the choana (the passageway between the nose and the throat) of tetrapods. Schultze rejects the homology on two grounds. The first is due to transformational methods, specifically topography. The physiology of the two features is not ‘similar’ in the correct respect. The other reason is due to cladistic parsimony, ‘taxic’ methods. Because a sister group of dipnoans lacks the nasal opening altogether, a tree which has the traits as parallel (independently evolved) is more parsimonious insofar as this tree postulates less evolution events (see next chapter for an explanation of this). “That means that homology is denied on two levels. The internal nasal opening in dipnoans fails the test of similarity in its position relative to surrounding structures and as a synapomorphy, i.e., not present in the common ancestor of dipnoans and tetrapods. (Schultze pp 163)”

Testing for homology occurs, then, twice in the process. Initially characters are considered topographically, roughly identically to how they would be by pre-Darwinian anatomists. So first we must judge (for instance) what counts as a prominent and nonprominent snout. As stated above, close similarity provides strong inferential grounds for homology, but as it is unable to differentiate between homology and parallel analogy it cannot be seen as a ‘recognition’ of homology.

Although the test for synapomorphy will not necessarily overturn the initial judgement, it frequently will. Judging how much either test should be weighted is determined by both the ‘closeness’ of the cladistic trees (see next chapter) and the closeness of the transformative similarity. As cladistics is probabilistic, there will be cases where the probabilities for a particular arrangement are indecisive. In such cases, we may prefer close transformative similarity. Unless there was some reason to give a lot of weight to the transformational ‘homology’ between choana and internal nasal openings, the test for synapomorphy would be enough to overturn the judgment, so long as the cladistic probabilities are strong. The transformational method quantifies resemblance-relations and at best gives

a strong, preliminary account of the homology of the states. It is only when the trees are constructed that we confirm or disconfirm the initial characterizations. Due to this, we should view the resemblance-relations, not the homology, as the primary phenomena.

So, to recap my account. I see the cladistic terms synapomorphy and homoplasy as separate from homology and analogy. The cladistic terms are definitions, which are determined using both taxic and transformative methodology. Homology and analogy are explanations of the similarities. The fundamental phenomenon of interest is the similarity between lineages. These similarities, in the appropriate circumstances, can be explained by some combination of continuity of origin (homology), continuity of process (analogy) and accident.

I have given three reasons to prefer my account over others, particularly that held by Griffiths.

1. The transformational account cannot distinguish between homology and parallel analogy. As a different suite of inferential uses apply to these we ought to prefer a theory which preserves the distinction.
2. My account coheres with a more general account of the explanation of similarity.
3. I have argued against granting epistemic privilege to the transformative or taxic account, claiming that we ought to use both streams of evidence to determine synapomorphy or homoplasy. Because both homology and analogy are pre-theoretical, an account which places one over the other will have a tension between the supposed epistemic asymmetry and the nature of the phenomena.

2.3 Glossary

Homoplasy: A definition from cladistics. A congruent character-state in two (or more) lineages is not present in the common ancestor of the lineages.

Synapomorphy: A *definition* from cladistics. A congruent character-state in two (or more) lineages is present in the common ancestor of the lineages.

Analogy: An *explanation* of homoplasy. A congruent character-state between two (or more) lineages is homoplastic and evolved due to those lineages occupying similar selective environments.

Homology: An *explanation* of synapomorphy. A congruent character-state between two (or more) lineages is synapomorphic and the state has been retained due to entrenchment in the developmental system (as opposed to maintained by selection).

Clade/Monophyletic Group: A phylogenetic tree including an ancestor and all of her descendants.

Character: A trait as defined by the transformational method. Human feet and Chimpanzee feet are both transformations of the character 'feet' in primates.

Character-State: A trait as defined by the taxic method. Some aspects of Human feet are in a particular character-state, Chimpanzee feet might be in a different state.

Before discussing the uses of homology and analogy in inferences in chapters 3 and 4, I want to discuss a potential misunderstanding that could arise in terms of analogy.

2.4 Function and Similarity

To close my account of homology and analogy I want to address two questions. First, it has been claimed in the literature that there is something odd about casting homology in functional terms, and analogy in non-

functional terms. I think this issue is easily resolved if we take function and physical description as being continuous. Second, I will use this discussion to (as promised) briefly tackle the issue of similarity-identification itself.

2.4.1 Function

We might be forgiven for thinking that a functional description of an object is separated from its physical description. There is a big difference between an abstract teleological definition ascribed to an object and a physical description of it. ‘Hammer’, it could be argued, is a functional definition which could be ascribed to anything which drives a nail-like object into a wall or post (anything which ‘hammers’).

Compare this to a physical description of a typical hammer:



In the functional case we determine that an object is a hammer because it meets some criteria of use; in the physical descriptive case an object is a hammer if it meets some criteria of description: it must have a ‘metal head’ or a ‘wooden handle’. *Prima facie*, these look like unrelated ways of ascribing the term ‘hammer’ to an object.

If we were committed to this dichotomy, then we might think there was something odd about the way homology and analogy have been discussed in the last two chapters. If we think a synapomorphy is a case of physical similarity between two lineages, whereas a homoplasy is functional similarity between lineages, we might wonder how it is that the same criteria could be used to identify them.

One place where this worry has become overt is in discussion of behavioural homologies (Love 2007, Rendal & Di Fiore 2007). A behavioural similarity is functional. Humans and birds ‘dancing’ to attract mates is similar insofar as both are using a set of movements in order to make themselves attractive to the opposite sex. However, a homologous similarity is supposed to be determined by physical similarity – not functional similarity! “[W]hat a structure does should not enter into an evaluation of homologue correspondence... The juxtaposition of ‘function’ and ‘homology’ is oxymoronic (Love, pp 693).”

These kinds of worries, in my view, are confused. There is not a dichotomy between physical and functional description – the two are continuous. This claim is found in Bill Lycan’s *The Continuity of Levels of Nature* (Lycan 1987), “...highly teleological characterizations... have the virtue of shading off fairly smoothly into (more) brutally physical ones. (Lycan, pg 53)” According to this view, the functional account of the hammer is at a ‘higher level’ of abstraction than its physical description. ‘More abstract’ simply means ‘towards the functional end of the continuum’. The physical parts of the hammer are made of components, the handle and the head, which are functional descriptions. The wooden handle consists of various carbon compositions in a particular arrangement, and the steel head a different arrangement of iron and carbon. The atoms could be thought of as playing functional roles.

Lycan argues for his position largely from example. A neuron, he points out, “... may be understood either as a physiological term (denoting a kind of human cell) or as a (teleo-) functional term (denoting a relay of electrical charge); on either construal it stands for an insatiable – if you like, for a role being played by a group of more fundamental objects. (Ibid, pg 57, italics removed)” A physical description of a neuron is still functional: it describes in terms of cell structure (which are functional roles played by atom-clusters).

Similarly, when we describe resemblance-relations between characters, be they homologous or analogous, they will be at a certain level on the continuum. When we say that the eyes of primates are topographically similar, we refer to the structure of primate anatomy – which is as a functional gloss over the various parts involved. The eye, bone, skin and so on consist of various cell-types playing different roles. We can see an analogous similarity, such as that between the shape of dolphins and sharks, in terms of organization and continuous with topography.

By my account of homology and analogy the target of explanation is the resemblance-relation. A resemblance-relation may be at any point of the

physical-functional continuum. For example, consider these similarities between myself and a platypus. We are both made of carbon atoms. We both have genes. We both have hair. We both have a four-limbed body plan. We both put resources into raising our young (although in my case this has not been tested). In describing these similarities we move from more physical description into more functional description.

These levels of description, however, are part of our initial investigation of the target similarity. Once we have determined whether the similarity is homologous or analogous, we then parse it in terms of phylogenetic ('physical') or selective (functional) terms. So it is our explanation, of the phenomenon, rather than its physical description, which determines their phylogenetic or selective status.

Alan Love (2007) has suggested that we should envision behavioural homology in terms of *activity-function* as opposed to *use-function*¹⁰. Use-function is a functional description which tells us what something is for, while activity-function is simply what something does. A clockwork watch is not designed to 'tick', ticking is a byproduct of clockwork. However, this does not mean that we cannot give a (activity-) functional explanation of why clocks have the capacity to tick. Similarly, my nose and ears were not 'designed' to hold my glasses to my face, but (given the design of glasses) this doesn't mean that the capacity of my face to balance glasses cannot be given a (activity-) functional explanation.

I whole-heartedly agree with Love's claims about function generally, but think he is wrong that homologous functions can only be activity-functions. To count as a homology, all we require of a resemblance relation between two lineages is it be held by their common ancestor and that the similarity is explained by descent. Where the resemblance relation sits on the physical-functional continuum is irrelevant for determining whether it is a homology

¹⁰ Following from the tradition of using non-selective accounts of function in biology as argued by Amundson & Lauder 1994.

or an analogy. However, it may be very important in terms of identifying the similarity in the first place.

2.4.2 Similarity

I can now turn to the issue of identifying similarity. I have so far taken it as given that we can correctly identify resemblance-relations. But with some apparent similarities it is not obvious how we make this claim.

Similarities in physiological characters seem straight-forward. Because we are discussing physical objects, similarities can be quantified (as they are in cladistics). The feet of chimpanzees and bonobos look more similar to each other than they do to our feet. And we can do better than simply observe – we can measure various dimensions and compare them. Although these quantitative measurements are not necessarily reconcilable with qualitative observation they can, at least in some situations, provide independent reassurance of the similarity. Things get tougher for less tangible traits, however.

In the introduction, I mentioned Marino et al (2008)’s discussion of convergences between cetacean and primate cognition. Here is what they have to say about dolphin cognition:

“Laboratory studies of bottlenose dolphins have documented various dimensions of their intellectual abilities. These include an understanding of symbolic representations of things and events (declarative knowledge); an understanding of how things work or how to manipulate them (procedural knowledge); an understanding of the activities, identities, and behaviours of others, (social knowledge); and an understanding of one’s own image, behavior, and body parts (self knowledge). All these capabilities rest on a strong foundation of memory; investigations have demonstrated that bottlenose dolphin auditory, visual, and spatial memory are accurate and robust. (pg 968)”

They go on to claim that “They [primates and cetaceans] are examples of convergent evolution of function largely in response, it appears, to similar societal demands (pp 971).” But their claim of cognitive

convergence rests on cetaceans being able to perform the same tasks as primates. They successfully mirror-recognise, for instance. There is a similarity in task-performance – but does this mean the cognition is the same?

Behavioural convergence is also problematic. A very contentious case is the claim that there is convergence between leaf-cutter ants and humans: agriculture (Conway-Morris 2003). A very coarse functional analysis of their behaviour renders a similarity, but is it truly convergence? How similar do two traits need to be before a convergence can be claimed?

I do not have an answer to this scepticism about similarity in behaviour and cognition, but I want to draw upon my points about function in the last section to suggest the right approach to an answer. The problem with identifying similarities in cognition and behaviour, as I see it, rests upon the functional nature of those similarities. In both the cetacean and the ant case the scepticism arises from the functional analysis which is required to describe the similarity. They look similar in terms of function, sure, but how do we know that the functional analysis we have undertaken is correct? Are we actually picking out a similarity, or is one being gerrymandered¹¹?

If I am right that physical and functional description is continuous, then the epistemic tasks of identifying similarity in morphology versus behaviour or cognition are not different in kind. As we shift from more physical phenomena to more functional phenomena our problem of identification is the same. In the foot-example above, for instance, how do we know which dimensions of measurement are important? Brute foot-size may be an unsuitable criterion as it is more than likely coupled to body-size (the same reason we measure encephalization as opposed to brute brain-size). We

¹¹ In the cognition case there is a further difficulty – the inference from the ability to perform a particular task to there being a particular underlying mechanism which is responsible for that capacity. See Andrews 2009 for a discussion of applying psychological properties to animals and Browne 2004 for philosophical scepticism of dolphin cognition-claims.

need a theory which tells us which dimensions of measurement are important. For (more) physical features we might rely on biomechanics, or neurology could suggest important features in brain similarity. For (more) functional similarities a different group of theories could be utilized – cognitive neuroscience, behavioural psychology, and so on.

So the identification problem exists along the spectrum, but it is much easier to solve for physical traits. An account of the identification of functional resemblance-relations would mirror the identification of physical resemblances. The more a similarity can be quantified, and the more traction that can be gained on the appropriate dimensions of similarity, the happier we should be with the identification.

2.5 Conclusion

I will quickly recap my account of homology and analogy.

Homology and analogy are both evolutionary explanations of resemblance-relations (character congruence) between biological objects. If the similarity is homologous, it is explained in terms of continuity of genotype due to continuity of descent. If it is analogous, we explain the similarity in terms of continuity of selective process.

The transformative and taxic accounts of homology are both inferential. The transformative quantifies the similarities on a one-to-one basis, whereas the taxic takes a holistic approach, using congruence to construct the most likely arrangement of evolutionary histories.

With this account in hand, we can now turn to the central problem I want to address, the use of analogy in inferences.

3. Epistemic Warrant & Causal Depth

The next two chapters will explain the problem of causal depth. Analogous similarities between disparate lineages are too shallow to gain epistemic warrant for the kinds of inferences I am interested in. They can support the possibility of a hypothesis, not the actuality.

I shall begin with a discussion of explanation. This will provide a framework which can explain the issue at hand. I will define what is meant by ‘epistemic warrant’ and give a general account of what constitutes a problem of causal depth.

The second half will apply this framework to inferences reliant on homology. As we shall see, homologous inferences are in fairly good shape, but I will suggest some instances where we should be cautious of them which will be built upon later on.

A useful way of understanding the argument in the next two chapters is in terms of Nelson Goodman’s concept of *projectibility*. A concept is projectible if it can be used in an inductive inference. If I am able to say that one object has a certain property, which is projectible, then I will be able to extend (project) that property onto other objects of the same type. The classic example is the difference between ‘green’ and ‘grue’. Something is grue if it is green when observed before a certain time (say, the 11th of January 2010) and blue when observed after that time. The observation that an object is green can be part of an inductive inference. Observing a green emerald, I might then claim that all emeralds are green. However, observing a green emerald before the 11th of January 2010 does not then allow me to infer that all emeralds are grue. Although an emerald’s being green prior to the 11th of January 2010 is consistent with emeralds being grue, because we do not have enough evidence we cannot support the inference. So, green is

projectible, but grue is not.

If the line of thought in the next chapter is right, then biological analogies are not projectible. Even if it is the case that a particular analogy exists – say, both sharks and dolphins evolved a stream-lined form due to the selective pressure of an aquatic environment, this does not then allow me to infer (project) that other lineages which occupy that niche will evolve a stream-lined form.

3.1 A Note on Explanation

This section covers some conceptual ground about explanation. It will provide some tools that will help us analyse the kinds of inferences I am interested in. I will first sketch two dimensions with which explanations can be analysed. These will then be used to give an account of what it is to have epistemic warrant, and define what we mean by ‘causal depth’.

A caveat: the account of explanation given here will be fairly rough and ready. For my purposes I just need to exposit a framework which can be used to discuss the underlying justification behind analogous inferences (their epistemic warrant) and why we might be suspicious of them. I will point to more philosophically rigorous work covering the terms I am employing and give as clear an exposition as possible. Before getting to the ‘dimensions’ of explanation I will employ I need to lay some groundwork.

We make inferences towards a particular *explanatory target*, the phenomenon under investigation. In the previous chapter, I argued that homology and analogy are explanations of resemblance-relations between biological objects. The resemblances are the explanatory target (the explanandum) which an evolutionary account explains (the explanans). I will mostly stick to a single explanatory target through this section, the ‘K-T Extinction’¹², so it will be useful to describe the phenomena.

The K-T Extinction refers to an event roughly 65 million years after

¹² Or K-Pg Event, now that the tertiary has been divided into the Paleogene and Neogene

which roughly 50% of marine genera vanish from the fossil record (Dawkins 2004 pp 256). It is best known as the event that marks the extinction of the dinosaurs. The K-T boundary is a geological formation boundary between the Mesozoic Era and Cenozoic Era. A striking feature of the boundary is the difference in fossil finds on either side. Underneath we find Mesozoic flora and fauna, above there are none. The explanatory target, then, is the disappearance of the Mesozoic fossils.

There are many questions we can ask about the disappearance of fossils at the K-T boundary. We could ask why the fossils themselves are evidence for living creatures, why they disappeared, why some lineages have survived, and so on. The different dimensions of explanation I shall outline are methods of categorizing these different questions.

Note that I am assuming pluralism (or ecumenism) about explanation. All of these explanations are interesting and important in their own right, and their use depends upon the needs of the particular question we want to answer. It is now time to introduce the first dimension of explanation.

3.1.1 Robust Process vs Actual-Sequence

A useful distinction found in Jackson and Pettit (1992) and in a biological context in Sterelny (2001) is *robust process* and *actual-sequence* explanation. These are modal terms: an actual-sequence explanation identifies "... the particular possible world that we inhabit (Ibid pp 131, italics removed)." Whereas a robust-process "... compares our world to others (Ibid, italics removed)." Applying this distinction to the K-T example, we can examine the 'Alvarez' theory (which claims that the extinction event was caused by a meteor-impact around 65 million years ago) in two senses.

An actual-sequence approach will tell us about the particular asteroid which hit. It might give us the size, shape, speed and trajectory of the object. The explanation may identify a particular crater (in the case of the K-T impact, probably the Chicxulub Crater in the Yucatan), and describe the particular species were eliminated because of the impact. In contrast, a

robust-process explanation might include information about the formation of craters, the tendency for asteroid impacts on earth and the tendencies of species with particular traits to become extinct in certain environments.

So while the actual-sequence will give us plentiful information about the actual event itself, a robust-process account will contrast our world to others. For instance, maybe the extinction caused by the impact was a stochastic event. Those ‘impact worlds’ which are at the same time (to within a few thousand years) would also contain the extinction, but those at different times would not. The size and position of the impact might make changes across worlds. Those where the impact is smaller, for instance, might be less likely to have extinction events. Theorizing, modelling and (where possible) testing these counterfactual instances can tell us about the probability of this event and others like it in the past.

3.1.2 Fine-Grained vs Coarse-Grained

Frank Jackson and Philip Pettit (1992) analyse explanation in terms of *grain*. The grain of an explanation is defined in terms of “...greater or lesser attention to the detail of the producing mechanism (pp163).”

A *coarse*-grained explanation will pay less attention to the producing mechanism. An extremely coarse-grained answer to the question of why no dinosaur fossils exist above the K-T boundary would simply be that the dinosaurs become extinct (and thus could not leave any fossils).

A *fine*-grained explanation focuses on the producing mechanism. So a more fine-grained explanation might claim there are no dinosaur fossils above the K-T boundary because (say) a 10 kilometre-diameter bolide (impact meteor) hit the Yucatan peninsula creating a ‘nuclear’ winter. A coarse-grained explanation will tend to be more general than a fine one, but

this is not necessarily the case¹³.

My discussion of physical and functional description from last chapter should map fairly neatly onto grain. A more functional description will tend to be of coarser grain than a physical one. This is because a functional description abstracts certain properties of the phenomenon in general terms.

If we take a selective-functional explanation, and increase the grain, we will see the explanation will become more ‘physical’. Perhaps part of the explanation of which lineages survived the K-T extinction event is that smaller sizes were better suited to the environment. A smaller animal requires less food, tends to have a shorter gestation period, and so on. Creatures that meet these selective-functional requirements are more likely to survive an extinction event. If we increase the grain to examine how these smaller animals may have survived, our description will become less abstract. The small mammals of the time, for instance, are well adapted for extremes due to their warm-bloodedness and the warmth of their coats. This is still selective, but now with more detail. At an extremely close grain, the adaptation falls out of the picture and we have particular stories about how particular individuals survived.

To recap, there are two ‘dimensions’ I will use to analyse explanation. We can analyse explanations in terms of grain. The richness of detail of an explanation, its proximity to the causal mechanism of the phenomena in question, sets grain. We can analyse them in terms of actual-sequence versus robust process. An actual sequence explanation tells us about the world we are in, while a robust process compares our world to others.

¹³ I believe an important factor in the difference between an adaptive and phylogenetic explanation is the functional nature of adaptation. There may be a trade-off between the level of functional generality required to get an adaptive (and particularly analogous) inference off the ground and a fine-grained explanation. However, the nature of this trade-off is particularly difficult to get a conceptual handle on and is not necessary for my account of the problem of causal depth. Matthewson & Weisberg 2009 give a very good account of this kind of trade-off focusing on formal modelling.

I see Robust Process/Actual Sequence and Fine/Coarse grain as (largely) independent dimensions of explanations. In the table below I compare four versions of the 'Nemesis' Hypothesis, introduced by Raup & Sepkoski (1984). This hypothesis seeks to explain the apparent pattern in extinction events on earth in reference to extra-terrestrial activity. By this hypothesis, extinction events on earth (including the one at the K-T boundary) are caused by impact events and their regularity is due to the sun having a companion star which disturbs the orbits of debris in the Oort cloud, sending them on a collision course with Earth.

So the table illustrates the kinds of explanations the dimensions I have outlined pick out. The explanatory target is: what explains the extinction event 65 million years ago? The fine-grained explanations include more information about the mechanism by which the impact event (or events) occur than the coarse-grained ones. The robust process explanations are in reference to the regularity of extinction events on earth, whereas the actual sequence focuses on the event 65 million years ago.

Figure v Explanations Plotted against Robust-Process/Actual Sequence and Fine/Coarse Grain

| | Fine Grain | Coarse Grain |
|------------------------|---|---|
| Robust Process | The sun has a companion star in an elliptical orbit which occasionally disturbs extra-terrestrial objects in the Oort cloud and sends them on a collision course with earth. The regularity of this event explains the regularity of extinction events. | There are regular impact events on earth which cause regular extinction events. |
| Actual Sequence | The sun has a companion star in an elliptical orbit which, sometime before 65 million years ago, disturbed a 10-kilometre meteor from the Oort cloud and sent it on an eventual collision course with earth. | 65 million years ago a meteor impacted with earth. |

These dimensions are not completely independent. For instance, as we shift from finer to coarser grains in a robust-process explanation, this can affect the number of possible worlds which are picked out. A coarser robust-process explanation of the regularity of impact events than the Nemesis Hypothesis might run as follows. Large bodies in space, such as planets, act as ‘gravity wells’ which attract smaller extra-terrestrial objects. Given the right conditions, these smaller objects can get caught in a ‘death spiral’ which results in an impact event. This explanation is coarser grained than the Nemesis Hypothesis because it does not provide as specific a causal mechanism. It does apply to a larger set of worlds, however. The Nemesis hypothesis might be true of solar-systems with twin stars (whether it is true of earth or not); whereas the explanation in this paragraph might be true of all solar systems. So as we shift to finer grain, adding more causal information, we sometimes restrict the number of worlds the Robust-

Process explanation refers to. Having said this, I think these dimensions of explanation are independent enough to justify their use here.

With this in hand, I will now sketch an account of how inferences and explanations are justified.

3.1.3 Epistemic Warrant

Epistemic warrant is granted when there is solid ground for a particular inference or class of inferences. Scientific inferences typically require commitment to generalizations, frequently from other sciences. We are comfortable with the palaeontological inference from fossil finds to ancient, living animals due to the underlying, geological processes of fossilization and rock stratification (and there will be at least a tacit assumption that these processes are grounded in some other theories). A particular inferential structure has epistemic warrant on two grounds. We must have good reason to think the premises support the conclusion; we must be happy with the robust process which the structure relies on. If an explanation, inferential structure or hypothesis has epistemic warrant it is ‘on the table’.

An explanation is epistemically justified based on two types of criteria: super-empirical virtues and underlying processes. We may prefer a particular theory because it exemplifies some virtue, such as simplicity or adequacy. These preferences give us reason to support one theory over another. We may, for instance, prefer the Alvarez theory of Mesozoic extinction over a different theory because it accounts for two phenomena: the increase in iridium at the KT Boundary (see below) and the extinction of the Metazoan fauna. Super-empirical considerations are less important for my account and so will be dealt with when I come to them in discussion, but the idea of an underlying process deserves attention.

An actual-sequence explanation will frequently rely on robust processes for justification. The Alvarez theory of the K-T Extinction is an actual sequence explanation as it tells us about events in the actual world; it is a hypothesis about what actually happened. However, our justification for

believing the theory is not derived from it alone. The main evidence for the theory is geological. The boundary contains ‘shocked’ Quartz (which is found in impact sites) and there are high levels of iridium deposits in the K-T boundary. Iridium is rare on earth, but common on asteroids. Here is the robust-process. When asteroids hit iridium-poor planets like earth with enough force, debris from the crater and the asteroid will coat the planet. This will leave a geological record of the impact-event. Those worlds with impact-events will have a line of iridium, those without will not. If we have reason to believe these geological robust-processes, then we have reasons to believe that there was an extra-terrestrial impact at the K-T boundary – an important part of the Alvarez actual-sequence explanation (see Jeffares 2008 for a more rigorous account of the relationship between an historical inference and its supporting theories).

The Alvarez theory could also inform a robust-process explanation. In Stephen Jay Gould’s *Wonderful Life*, for instance, he argues that evolution’s path at the macro-level is massively contingent due to external disruptions to life’s development (Gould 1989). Perhaps asteroid impacts of the size required to wipe-out world eco-systems are a (relatively) frequent occurrence on earth. Moreover, the timing of particular extinction events on earth is an important aspect of the Nemesis Hypothesis. Examining the scope of the damage caused by the impact at the K-T boundary and other impacts could form the basis of a robust-process theory such as Gould’s contingency thesis or the Nemesis Hypothesis. That, for instance, there have been major impacts which do not coincide with mass extinctions suggests that there are other factors at play here.

So actual-process explanations rely on robust-processes for justification, and can act as data-points for justifying robust-process explanations. They may boot-strap: a particular process may explain a sequence which is in turn evidence for that process.

I am now in a position to state my first pass at how we provide an epistemic warrant for a particular inference. A particular explanation gains

its epistemic warrant from its relationship with other explanations and theories. When we examine a particular epistemic practise, we should do so in terms of these relationships. The Geological practice of reading strata as temporal order is grounded in other geological theories. Different kinds of rock will have a particular signature deposition. Silt will indicate the past presence of a river, coal a swamp, and so on. They explain this in reference to a general theory about how environmental features will affect the rock deposits. If geologists are correct in their explanation of rock formation, then that feature of rocks should be projectible onto the rock in strata. Inferences which read temporal order from rock strata, then, are justified (in part) by the relationship between the theory of rock formation and the strata themselves. So epistemic warrant is concerned with how well supported a generalization is, and its scope: what kinds of events it applies to. There are two more points I need to make about epistemic warrant.

Although epistemic warrant can be thought of as a property of a particular hypothesis, it is much clearer when taken as contrastive between two (or more) hypotheses. Say we are comparing two hypotheses about dinosaur extinction. In the first (H1), the extinction was, at least in a large part, caused by the impact event. In the second (H2), the impact event happened after the extinction which was caused by (say) large-scale ecological change due to the shifting of tectonic plates. The epistemic warrant for H1, as opposed to H2, consists of both evidence and theory which relates the evidence to the hypothesis. So, that there is a large impact crater off the Yucatan peninsula; and this crater is dated to around 65 million years ago; and the size of the impact would be large enough to create the kind of world-scale carnage required of a mass-extinction event based on impact modelling; are all pieces which count towards the epistemic warrant which favours H1 over H2¹⁴.

¹⁴ I do not mean to say here that H1 or H2 cannot both be in part right, I am simplifying for the sake of the example...

Epistemic warrant could be thought of in two ways. A particular inference may lack warrant due to a paucity of evidence. We may dislike the Nemesis hypothesis because we are not convinced of the observations which support it, or feel that the observations are not sufficient. In this sense warrant is a relation between a hypothesis or explanation and its evidence. Alternatively, a hypothesis may be unwarranted because some underlying process or theory which the hypothesis relies upon does not do the work required of it, or if the theory is not sufficient to explain the effect. So we may be unhappy with the Nemesis hypothesis because the gravitational theory it relies on is incorrect. Or, because collision events do not always cause mass-extinctions, the Nemesis Hypothesis cannot be a complete explanation. Here warrant is a relation between a particular hypothesis and its supporting theory. It is in this latter sense that I will discuss epistemic warrant. So a theory lacks epistemic warrant if a supporting theory is not sufficient to support it.

And so, when we judge the epistemic warrant of a particular hypothesis, explanation or regularity, we examine a) the observed evidence which supports the theory; b) the robustness of the supporting theories/underlying processes (whether they are projectible). Epistemic Warrant is granted if the evidence for the theory is strong enough, and if the underlying processes are sufficiently robust – if the concepts employed in each process are projectible. But not all processes are created equal. Eliot Sober (Sober 1988) makes a useful distinction between a process being information-destroying and information-preserving.

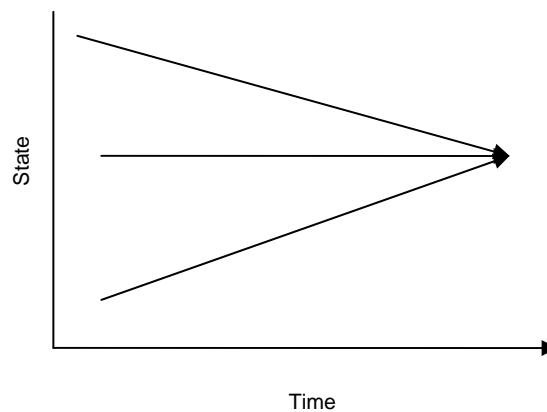
3.1.4 Information Preservation and Destruction

There are some processes whose reach from the past is weaker than others. Those weaker processes sometimes provide weaker epistemic warrants. I am introducing Sober's distinction here in order to exposit a continuum that will allow me to explain the problem of causal depth.

If a process equilibrates, which is to say that all initial conditions lead to the same state, then it is *information-destroying*. When we observe the final

state, there is no way for us to infer the history of the process. Sober's example is of dropping a ball into a (perfectly regular) bowl. The ball, after spinning back and forth across the surface, will always come to a rest in the centre of the bowl. Once the ball has stopped moving, we can no longer infer its original position from its final state.

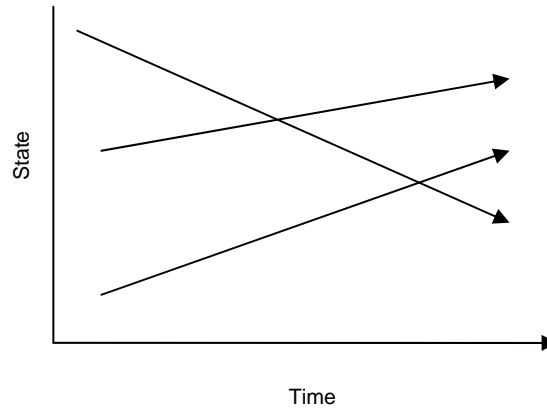
Figure vi Information Destroying Process



The process equilibrates – the past cannot be inferred because all initial conditions end in the same state

If a process has several local optima that are gravitated towards dependant on initial conditions, then it is *information-preserving*. Imagine the bowl is not perfectly regular, but has several dips in its base. It might be the case that releasing the ball at a particular position will increase the probability of it coming to rest in one or the other of the dips. If this is the case, then we could make inferences about the initial state of the ball from its final resting place.

Figure vii Information Preserving Process



The process has local equilibria – the past can be inferred

Information preservation or destruction is not a property of an explanation, but of a process. It is not due to a lack in our epistemic abilities that we cannot infer backwards from a perfectly information-destroying process. If we had absolute causal knowledge about states at the end of the process, we would be in no better position to work out the initial conditions than we are in our epistemic poverty. As Sober puts it, “The fault... is not in ourselves, but in the bowl (Ibid pp 4).”

A process may be information preserving or destroying either in virtue of the process itself (as Sober describes it) or in virtue of its relationship to other processes. One process might interfere with another, creating noise which destroys whatever traces the latter process may have left. The process of stratification leads to an identifiable, recoverable sequence which Geologists can use to delineate time periods. Stratification is information-preserving. Noise can be created by processes such as mining, metamorphic transformation and erosion. These erase the signal of temporal order from stratification by re-organizing them. No matter what order the rock was layered, the end result would not be recoverable because the order has become confused. We would then be unable to delineate the differences and

infer a temporal order from the rock.

So there is a relationship between epistemic warrant and how information-preserving an underlying process is. If the process falls towards the information-destroying side of the spectrum, some inferences which rely upon that process might lack epistemic warrant. Claims relying on information-destroying processes may not be projectible: the observations we take will not ground inductive inferences. Once I have examined how this might affect the kind of grain available to an explanation we will have the problem of causal depth.

3.1.5 Causal Depth

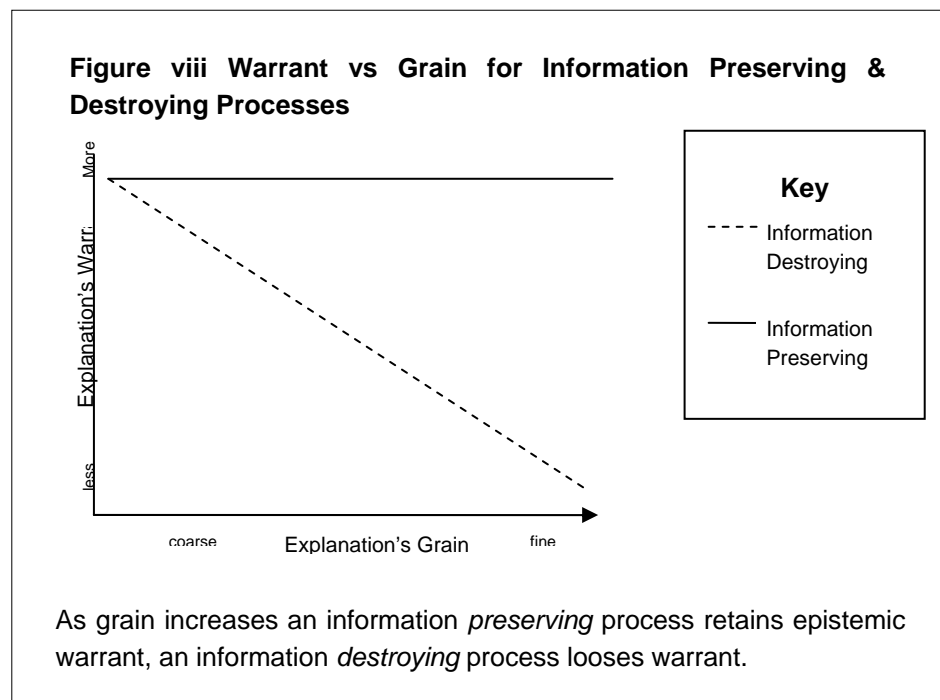
A problem of *causal depth* arises when an explanation requires a particular grain, and the underlying process we rely on is too information-destroying to 'reach' that grain. By examining the relationship between the grain of an explanation and information-destroying processes, the problem will become apparent.

A destructive process will sometimes limit available grain. Slight and ambiguous, traces might not provide the right information to allow choice between hypotheses. Although geological structures like the K-T Boundary do provide a temporal order to events, they are less effective in providing temporal scale. Does the increase in iridium mark an event of a few hundred years, a few thousand, or a few million? The process of stratification is fairly information-destroying in regards to this question. As layers compress, the traces we could use to delineate time-scale are destroyed. Without a fine-grained timeline, we may be unable to choose between hypotheses.

Consider two versions of the Alvarez Hypothesis. One theory claims that the dinosaurs were wiped out quickly over a few hundred years by the impact. The other claims the dinosaurs were already in decline and the impact exacerbated events; the extinction was drawn out over millions of years. Both hypotheses agree on a coarse-grained version of the Alvarez theory: the K-T extinction was due to a meteor impact. Their differences

emerge when we increase the grain. If we cannot find a means of setting the likely time period of the extinction event because stratification is information-destroying in regards to time-scale), then we lack epistemic warrant to choose between the two hypotheses¹⁵.

The more information-preserving a process is the more likely it can be used to decide between rival hypotheses. An information-destroying process, however, might lose warrant as finer grains are required of it – it will not help us choose between rival hypotheses¹⁶.



So finally I can account for what it is to lack Causal Depth. When a

¹⁵ Sometimes of course independent information can be used to make these finer delineations. I do not mean to suggest that we cannot find means of answering this question, but rather that if stratification was as information destroying as I described it, then we would need to rely on different processes. Our grain cannot be increased relying on that process *alone* (see note 5).

¹⁶ This discussion is importantly impoverished. As the historical sciences do not usually rely on a single stream of evidence, one process' ambiguous traces could be taken in tandem with another's to construct a warranted theory (Jeffares 2008). This point will be expanded in due course.

particular process is information-destroying, either self-reflexively (as in Sober's bowl case) or due to noise, then it might lack the causal depth required to justify fine-grained explanations or inferences relying upon it. When comparing two or more hypotheses, the evidence we have points equally towards either hypothesis. In the previous example where we considered two versions of the Alvarez hypothesis, the process of stratification lacked the causal depth to let us choose between them. As we shall see this is the problem with analogous inference due to its reliance on adaptation.

3.1.6 Glossary

Actual-Sequence/Robust Process: A property of an explanation which sets its modal limits. An actual-sequence explanation tells us about the actual world, whereas a robust process contrasts the actual world with others.

Causal Depth: A property of a process which measures its level of influence on phenomena. An information-destroying process will have low causal depth. Explanations which rely on processes with low causal depth might lack epistemic warrant.

Course/Fine Grained: A property of an explanation which sets how much attention is paid to the mechanism which produces the target phenomenon. A course-grained explanation tends to be more general, functional and abstract and is more amenable to robust-process explanations. A fine-grained explanation is close to the mechanism, it tends to be more specific, physical and amenable to actual-sequence explanations.

Epistemic Warrant: How much credence we give a particular explanation or explanatory technique, particularly when compared to rivals. It is typically granted on the basis of the underlying processes and observations which support the explanation. (I will speak of it as) A relation between a particular hypothesis and the underlying processes it relies on.

Information-destroying/preserving: A property of a process which measures our ability to infer backwards to an initial state. The more information-destroying a process, the more difficult it is to infer back from it. A process may be information-destroying by its own accord, or due to noise.

Noise: When one process' signal is interfered by another it may make that process information-destroying.

3.2 The Epistemic Warrant of Homology

This section will explain what underlying processes ground homologous inferences. A homologous inference relies upon homology to explain a phenomenon. For instance, explaining my father and I's red-beardedness in terms of common descent is a homologous inference.

Homologous inferences gain epistemic warrant in virtue of two related concepts. One is an underlying process, which I will call *developmental entrenchment*. In most situations traits remain homeostatic across evolutionary time. The other is *cladistic parsimony*, which itself relies on a commitment to developmental entrenchment. By minimizing the number of hypothesized evolution events in a proposed tree (using iterated congruency tests) we can identify the most likely evolutionary paths for lineages and traits.

I will take each concept in turn. First we shall see how developmental entrenchment justifies homologous inferences. Second I will illustrate the role of parsimony in setting phylogenetic relationships between lineages.

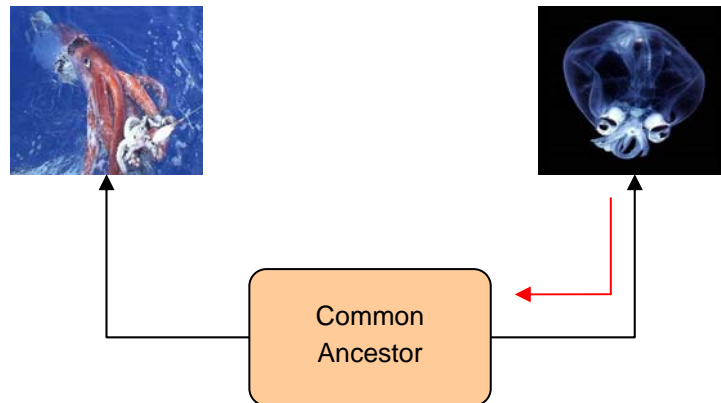
Colossal Squids are the largest known invertebrates, averaging around 13 meters long. Despite their bulk, they are extremely difficult to study due to their rarity and their environment. They occupy great ocean depths where the darkness and high pressure makes observation and collection of samples near impossible. Some traits are particularly inscrutable: how do Colossal Squids behave? One route that scientists take to answer these questions is to use the remarkably named Googly-Eyed Glass Squid (a tiny

transparent relative) as a proxy¹⁷. What justifies the assumption that an enormous, rare sea monster which hunts large fish and is preyed upon by Sperm Whales behaves like an insignificant transparent speck in the ocean? The explanatory target is Colossal Squid behaviour. The hypothesis is that they behave like Googly-Eyed Glass Squids. So, which underlying processes are pertinent to setting epistemic warrant for the hypothesis? The short answer is that the squid are closely related, and so we should expect many characters (including behavioural ones) to be homologous, but the inference is more complex.

The assumption that we can use relatives of the Colossal Squid to model its behaviour is based upon a two-step inference. Both steps are reliant on developmental entrenchment. In the comparatively recent past, the Colossal Squid and the Googly-Eyed-Glass Squid shared a common ancestor. They, with the other Glass Squids, form the clade *Cranchiidae*. If it is the case that most traits are homeostatic, developmentally entrenched, then any behaviour exhibited by a member of *Cranchiidae* was most likely present in the ancestor of the clade. So the first part of the inference is a retrodiction: traits held by a relative of a target species were most likely also held by the common ancestor of the target species and its relative.

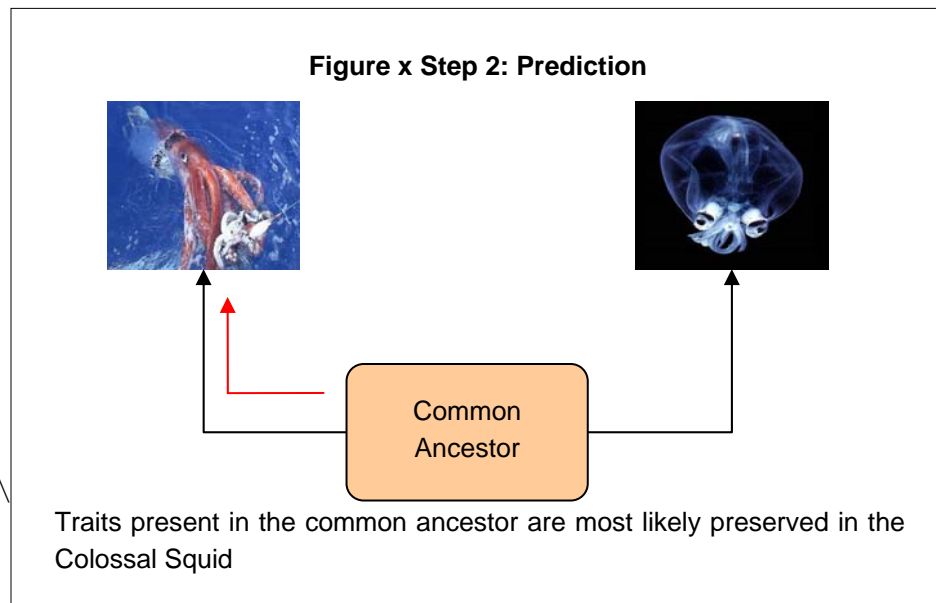
¹⁷ This example is taken from Te Papa's Colossal Squid display. Sadly, I have been unable to find any scientific papers which specifically mention this particular application of analogous inference.

Figure ix Step 1: Retrodiction



Google-Eyed Glass Squid (right) traits were most likely also traits of the most recent common ancestor of the Googly-Eyed Glass Squid and the Colossal Squid (left).

The second step is a prediction to the target lineage. If it is the case that a recent ancestor of the Colossal Squid exhibited a behaviour, then we would expect the Colossal Squid to also exhibit that behaviour. This again relies on the idea of developmental entrenchment. So the epistemic warrant of hypothesizing that behaviours exhibited by the Googly-Eyed-Glass Squid will be exhibited by the Colossal relies on most traits remaining homeostatic, at least over short periods of evolutionary time. A homologous inference gains epistemic warrant from developmental entrenchment.



Developmental entrenchment does not require that phenotypes never change, but that they tend not to. In order for the ‘descent with modification’ clause in evolution to work genotype must, on the whole, be largely static. Too much modification, and there is no longer a target for natural selection to act upon; natural selection requires traits to be heritable. So developmental entrenchment is a reasonable process to postulate. The inference is probabilistic: it is most likely that any particular section of genotype (and corresponding phenotype) will be homeostatic between generations.

In the example above I have assumed that the evolutionary relationship between the two squid is already set, but upon what basis do we postulate their phylogenies? How do we know, for instance, that the googly-eyed glass squid’s squid-like properties didn’t evolve independently the colossal squid’s? They could be homoplastic. As Sober 1988 shows a special similarity should guide these decisions. If the two squids evolved their similarities separately, this would require many more ‘evolution events’ than if they have a common ancestor. So the homologous hypothesis is more parsimonious.

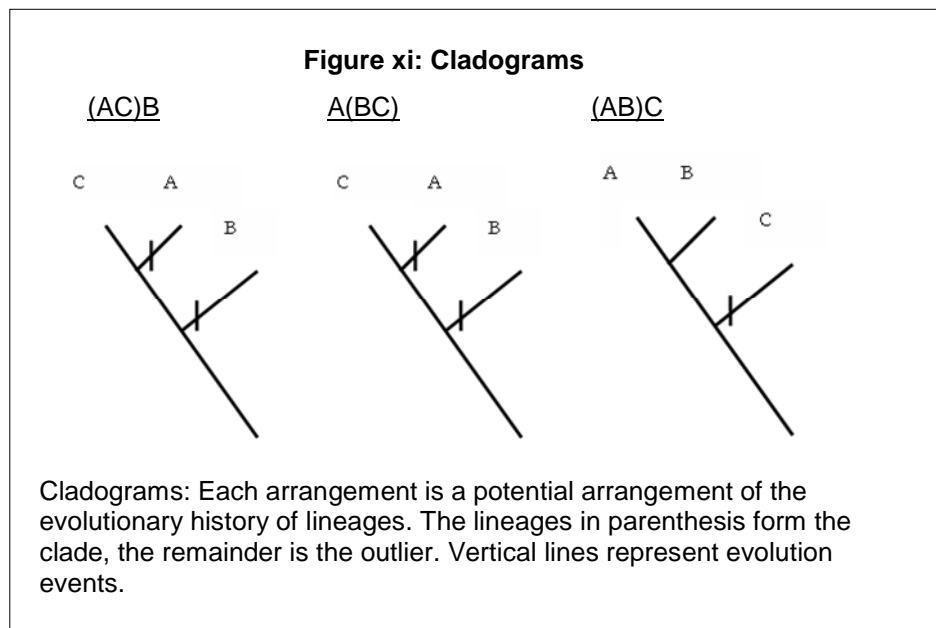
Parsimony's epistemic power in homologous inferences is clearest in cladistic practice. Cladistics identifies the most likely arrangements of relatedness between lineages. The basic method involves "[i]dentifying improbable associations of similarities in the overall space of variation, and then comparing likely explanations for their congruence (Franz 2005) p499." Relatedness is inferred using each trait congruence as a data point. For instance, one reason we think primates form a clade is their forward-facing eyes – the group is united by this trait – but the real story comes from comparing this congruence with many others and then constructing possible trees of relatedness (iterated congruence tests). Those trees with the least evolutionary events are the most parsimonious and are considered the most likely to be true.

Evolutionary relationships are set by comparisons of at least three lineages. The inference tells us which species has the most distant common ancestor of three, which is the out-group. This method is what Sober calls 'cutting'. The other two species will be part of (some) clade which does not include the out-group. This is set by a comparison of character polarity – whether they are derived or ancestral (as termed by the transformational method). Generally a very large number of character states are compared to set the relationships (in Schultze 1994, 216 are examined), but to exposit the basic structure of a phylogenetic inference setting evolutionary relationships I will use a toy example.

Compare our previous two species, the Googly-Eyed Glass Squid (A) and the Colossal Squid (B) with some other cephalopod, say some species of octopus (C). There are three possible phylogenetic arrangements: the two squids may be the closest related, expressed as (AB)C, the octopus and the googly-eyed squid may be the closest (AC)B, or the googly-eyed squid might be the out-group A(BC). Which arrangement is the most likely is based on which, based on character polarity, postulates the least evolutionary events.

Keeping the toy-like nature of the example, I will consider just three

character states provided by Boyle & Rodhouse: “The octopuses are clearly separated from the squids and cuttlefish on the basis of the number of arms, the lack of chitinous sucker rings and sucker stalks... (Boyle & Rodhouse 2005, pp 75). All three of these character states are held ancestrally by A & B, but are not held in C. Based on these three characters we can see that both (AC)B and A(BC) involve two evolution events. C (the octopus) is the ancestral form, and the two squid lineages have independently evolved their common traits. In (AB)C, however, there is only a single evolution event required – the squid form is ancestral and the octopus evolves as an out-group. This last hypothesis, with only a single evolution event, is the most parsimonious and so ought to be considered the most likely¹⁸.



Now imagine we have a character which is the same in both the Googly-eyed Squid and the octopus, but not in the Colossal Squid, say both

¹⁸ This is clearly *very* much a toy example – I am not suggesting that squid is actually the ancestral form, we would need to examine many more characters and lineages to make this claim. Sober 1988 contains a significantly more detailed and careful exposition of the inference.

use ink. This does not effect (AC)B but it makes A(BC) contain an evolution event at every branch and adds an event to (AB)C. This arrangement can be demonstrated in a chart (as below) where the character polarity is demonstrated by ‘0’ (ancestral) and ‘1’ (derived).

Figure xii Character States

| | A | B | C |
|---------------------|----------|----------|----------|
| 8 Arms | 0 | 0 | 1 |
| Sucker Rings | 0 | 0 | 1 |
| Stalks | 0 | 0 | 1 |
| Ink | 1 | 0 | 1 |

We can see from the chart that we have three ‘001’ arrangements and one ‘101’. Our two competing arrangements are (AC)B, where we would postulate that the evolution of the first three traits are homoplastic and the ink character is homologous and (AB)C where the ink is homoplastic and the other are homologous. In this case we can see that because the (AB)C arrangement minimizes the homoplasy, it is still the preferred arrangement. But why should we consider the most parsimonious tree most likely?

Sober (1988) applies the Principle of Common Cause to justify the use of parsimony in this case. As mentioned in the last chapter, the principle of common cause states that similarity (correlations) should be explained by postulating a common cause for that similarity. In my discussion of similarity in the last chapter, I downplayed ‘accident’ as an explanation in favour of continuity of history or of process based upon this principle. If two phenomena are (improbably) similar, it is probably because they have similar histories either due continuity of origin or process. But this does not get us any further for my purposes, as an analogy is as much a common

cause as a homology¹⁹.

However, if we examine developmental entrenchment, we can see that if phenotype is usually preserved across generations, then there should be more synapomorphy than homoplasy. In my octopus versus squid example, we should take (AB)C to be the most likely because evolution events are uncommon compared to phylogenetic homeostasis. As stated above, developmental entrenchment is a necessary component of evolutionary theory so it seems reasonable, based on the apparent success of the theory, to take it as given.

So, in my view, cladistic parsimony is reliant upon evolutionary theory. We need to know which evolutionary changes are more or less probable in order to conclude that an account which minimizes homoplasy (as opposed to one which simply takes the most overall similarity) is the right approach for phylogenetic reconstruction. The principle of developmental entrenchment does this work.

Homology is not immune to problems of causal depth. If species are very closely related the value of parsimony is stretched, as we saw in Schultze's discussion of lungfish in the last chapter. Differentiating homology and homoplasy (analogy) based on character-states relies on there being enough difference in the characters to delineate them. The requirement is extremely fine-grained when considering closely related lineages and it is questionable whether cladistic parsimony provides it (that there are continuing arguments between systematists attests to this). This is an issue when deciding between a hypothesis of parallelism or homology – because parsimony's power is weakened in these cases we may be unable to judge between them.

When attempting to discover the evolutionary relationships between

¹⁹ Sober goes on to develop a probabilistic framework to justify phylogenetic inference. For my purposes I just want to point towards the justification, as I have different fish to fry in discussing analogy.

very disparate lineages there are also issues. Developmental entrenchment becomes less information-preserving as the distance between the lineages in question increases, as the signal has more chance of being infected with noise from mutations. Very distant lineages are not just dissimilar in turns of character-state, but in character. What dimensions ought to be used to compare a prokaryote to a platypus? Because of this, claiming the relations between distant ancestors (say, whether *Chromalveolates* or *Rhizaria* are closer related to the rest of the eukaryotes) is extraordinarily difficult (Dawkins 2004pp 536-542).

Additionally, if the character states we are examining are particularly labile then developmental entrenchment and cladistic parsimony become less reliable. As Franz points out, “Character states with excessive rates of evolution, combined with deceptive biases in the abundance of homoplasy and a paucity of states – are unlikely to yield accurate phylogenies when parsimony is used. (Franz 2005 pp 501).” These issues will be returned to next chapter. Within the boundaries of the very closely related and the very distantly related, and given a reasonably placid evolutionary rate and enough data, however, homology is in good shape.

So, homologous inferences gain epistemic warrant from developmental entrenchment and parsimony. They are well founded themselves, and so we should be happy with inferences relying on them. The predicates of homologous inferences are (usually) projectible.

In the next chapter, I will discuss the epistemic warrant of analogous inferences and explain the problem of causal depth in this case.

4. The Problem of Causal Depth in Analogy

This chapter argues that the epistemic warrant of analogous inferences is reliant upon Natural Selection. It is necessary for Natural Selection to robustly fit phenotype to niche in order for analogous lineages to be used in comparative inferences. I will then argue that natural selection does not support analogous inference.

4.1 The Epistemic Warrant of Analogy

I will apply my account of epistemic warrant to inferences relying on analogy. Usually analogies are used to provide evidence for some robust-process in order to inform an actual sequence explanation. One reason to care about dolphin cognition, for instance, is that it could inform a general story about the evolution of cognition. This story could then generate hypotheses about how cognition evolved in other lineages. Analogous inferences gain their epistemic warrant in virtue of the process of Natural Selection. As we shall see, if Natural Selection fits form to function (if Adaptationism is true), then we should be confident of analogous inferences. I will give an account of Natural Selection and Adaptationism, and then show how it relates to analogy.

4.1.1 Natural Selection & Adaptationism

This section will explain what I mean by Adaptationism, so it can be linked to analogy in the next.

Peter Godfrey-Smith (1996) distinguishes between two explanatory approaches to biological form. An *externalist* approach explains phenotype evolution in relation to its environment. It is associated with Adaptationism. An *internalist* explains phenotype in relation to intrinsic properties. Evolutionary Developmental theory (Evo-Devo) is internalist. I distinguish

between internalism and externalism as explanatory projects and causal theses. An *explanatory project* is a set of questions, and an approach to answering them. A *causal thesis* is a claim the world; it is the fact of the matter, not an explanatory approach.

There are, then, two senses of internalism and externalism. First, they are explanatory projects. Several philosophers have pushed explanatory pluralism between Evo-Devo and Adaptationism (Brigandt 2007, Sansom 2003, Sterelny 2007, Amundson 2005). Their difference lies in the kinds of questions they seek to answer; there are particular phenomena they seek to understand and particular ways they seek to understand them. Adaptationism explains how traits become fixed in a population. Evo-Devo seeks to explain evolvability – the actual mechanisms of phenotypic variation. If we want an actual sequence about, say, how the hominid lineage became bipedal, the two approaches will give very different answers. An Adaptationist explanation will assume a particular pool of possible variation and explain how some variants become more predominant in a population. An Evo-Devo explanation will tell us about the developmental changes which caused the phenotype change.

Internalism and externalism can secondly be understood as causal theses. By externalism, the most important causal factor in forming phenotype are extrinsic features: the relation between the phenotype and the environment. By internalism, the most important causal factors are intrinsic features of the developmental system itself. There is, to some extent, a normative connection between these two readings. If externalism as a causal thesis is true, then we might be tempted to say that the best explanation of phenotype is Adaptationism. And if internalism is the case, then Evo-Devo explanations ought to be preferred. This is much too simple: a full explanation of how phenotypes evolve will incorporate both internal and external elements. But the point here is that given a certain question, an internalist or externalist approach might be more appropriate, depending which does the most causal work in that case.

Note that the kinds of explanations I am interested in here are ultimate, rather than proximate. I want to know whether the developmental process or selective process has more causal efficacy in shaping phenotype over evolutionary time, not the lifetime of a particular organism.

I will now focus my exposition on externalism: Natural Selection and Adaptationism. As a causal thesis, Adaptationists believe that the external process of Natural Selection has the most causal force in determining phenotype. As an explanatory project they explain evolutionary change in terms of the relationship between phenotype and selective environment.

Natural Selection is a process whereby successive forms are fitted to, and modify, a selective environment. Some individuals in a population may have traits which give those individuals an advantage over their peers. If this advantage increases the chance of that individual's offspring surviving and themselves reproducing at a greater rate than other members of the population, and if that advantage can be inherited by those offspring, then over time the advantage will spread throughout the group. Those individuals who are less fit (who on average produce less or less successful progeny) are weeded out of the population.

Generally, which traits increase fitness is context-dependant. A trait which increases success in one environment may not in another. For instance, increased running speed does not help a burrowing animal, nor is better eyesight. Having more efficient digging apparatus and a keener sense of smell or touch, however, might well infer an advantage. Because of this, animals in similar environments will tend to move in similar evolutionary directions - they will come upon the same solution to the same problem.

If Natural Selection does in fact shape phenotype, then identifying the relationship between trait and niche could form the basis of an inferential conditional of the form 'trait y evolves only if environment x is present'. This inference can be both predictive and retrodictive. If an animal lives in a certain environment, then we can predict that they have evolved, or will evolve, a particular suite of traits. An animal living in a burrowing

environment will evolve good hearing and touch, but eyesight will be neglected. We can also infer the environment a lineage lives in, or has lived in the past, based on their traits. The vestigial wing of the kiwi shows that in the past their environment was the air, not the undergrowth. This is 'reverse engineering' (Griffiths 1996), and is an important aspect to an Adaptationist approach to evolution.

Adaptationism, taken as a causal thesis, claims that selection shapes a lineage to a particular selective environment largely unaffected by the phylogeny of that lineage. This is to say that there are particular solutions to adaptive problems to which Natural Selection will drive phenotype towards irrelevant of the past history of that lineage. The scope of Adaptationism as an explanatory project is constrained by Natural Selection's causal efficacy. If it turns out that Natural Selection has minimal causal efficacy, then we may still ask Adaptationist questions, but the answers we receive will lack explanatory potency.

I will rehearse an informal example in order to illustrate the explanatory project of Adaptationism and set us up for the next section, where I will examine the relation between it and analogous inferences.

The males of some species of parasitic fig-wasps are both extremely violent and heavily armoured (see West et al 2001 for an academic treatment, Judson 2002 and Dawkins 1996 for popular accounts). After hatching they fight to the death, leaving a single survivor who monopolizes breeding opportunities. This behaviour is rare. Typically competition between males for breeding takes a non-violent, or at least non-lethal, form. The competing wasps are usually brothers, against our usual assumptions about kin-selection²⁰. According to Hamilton's Rule, for instance, individuals ought to show less aggression to their close relatives (See the discussion of Hamilton's Rule in West et al 2001). So the adaptive question is: how would violent and armoured traits spread throughout fig-wasp

²⁰ Although not too much; siblicide is not uncommon, particularly in birds.

populations? Given a better armoured or more violent variant, under what conditions would that variant be more successful?

An externalist answer to this question will be in terms of phenotype interacting with the selective environment: given a particular niche, violent behaviour and armour will be selected for. We need to cash out the costs and benefits of the traits given the wasps' lifestyle. Mate choice through duelling to the death is extremely risky, if you lose a fight then you lose any mating opportunities you could have in the future. This is why most male-male competition is reticent. If the mating opportunities are extremely limited, however, the nature of the game changes. In a one-shot mating environment, then saving yourself for a later 'date' is a waste of effort. In these fig-wasp populations females leave the fig never to return after mating so males have a single mating opportunity. In this situation, males who are more violent, who are willing to take more risks in competition with others, will do better than their more cowardly foes. In such a situation, anything which gives a physical advantage in combat such as armour would also infer a selective advantage. Fig-wasp males are nasty because the one-shot nature of their breeding environment favours nastiness.

So Adaptationism as an explanatory project relates phenotype to niche. An adaptive question asks how a particular suite of traits came to spread throughout a particular population. An adaptive solution explains that the lineage in question exhibits the traits because they maximise fitness given the niche the organism inhabits.

The appropriateness of this explanation depends upon the causal thesis of externalism. Any particular adaptive (actual-sequence) hypothesis relies upon the robust-process of Natural Selection being true for that case. It must correctly map onto the world; it must be that those traits are beneficial given the environment and true that those traits will be selected for and thus invade the population in question. It also depends on internal factors: even if the adaptive model is right, it can only come into play if there is the right supply of variation. The more causal efficacy selection has in that case,

the more epistemic warrant it grants the approach.

In Adaptationist explanation, a selective relationship is identified between a particular environmental variable and a particular function. To be justified, the inference will pick some regularity between environment and phenotype which holds true across relevant counterfactual worlds – in short, a robust process. So an adaptive model is a modal claim about how design space is constrained by selection. An adaptive inference applies the model to particular case or class of cases.

So, an adaptive inference or explanation derives epistemic warrant from the causal thesis of externalism. I can now relate this to analogous inferences.

4.1.2 Analogous Inferences

The purpose of this section is to connect what I have said about adaptive inferences generally to analogies in particular. An analogous inference is a special case of an adaptive inference. As we shall see, if externalism about biological form is the case – if the interaction between environment and phenotype do most of the causal work in the shaping of phenotype, then epistemic warrant is granted to analogous inferences.

An analogous inference takes information from one lineage to inform us about another. Sometimes when making inferences about the evolutionary history of a particular lineage we will draw on information from other lineages which are not particularly closely related to our target. We generally do this in cases where the closest relatives will not be much use. It is not obvious how examining the land-based extant relatives of, say, a sea-going reptile such as a plesiosaur would shed any light on its behaviour. However, perhaps the behaviour of species which now occupy the same niche as the plesiosaur would help. Although dolphins and sharks are not closely related, they do share morphological characters. Because their similarities are independently evolved (they are analogous), they could count as data-points for a robust-process about the conditions required for their evolution. If these similarities are due to the three lineages occupying the same selective

niche, then maybe they can inform an inferential model which reconstructs the lifestyle of the plesiosaur.

Analogous inferences also inform adaptive models. An analogy consists of similarities between both the traits of two lineages and their selective environment. As adaptive explanation postulates a causal connection between phenotype and environment, analogies could be seen as ‘natural experiments’ which test adaptive models.

So, one relation between analogous inferences and Adaptationism is that analogy can be used to test an adaptive inference (Workman & Reader 2004, Sterelny & Griffiths 1999). If a particular actual-sequence relies on a robust process for justification, then we should expect that generalization to be true in other cases. So one way we can test an adaptive hypothesis is to examine other lineages which occupy the same niche. If we can point to other examples which fit the model then it is corroborated.

In the fig-wasp case, the model claimed that one-shot breeding environments will select for armour and violence in males. Judson (2002) cites two corroborating examples. “Annual” fishes that live in transient puddles fit the model. Because their life-span is dependant on the existence of the puddle they were born in (only roe survive the long dry-season between rains) they only have one mating season. They exhibit extreme male-male aggression and sometimes fight to the death over females. Gladiator Frogs also meet the requirements of the model. They live for a short time – only a single mating season – and so have limited opportunities to mate. Not only are males aggressive towards each other they have also evolved a sharp, retractable spine which is used only in male-male combat. These independent evolutions of analogous traits corroborate the postulated regularity about one-shot breeding environments. Our confidence in the regularity will also infer confidence in the particular hypothesis about fig-wasps.

Falsifying evidence is somewhat problematic in adaptive models. Judson does not consider any cases where a lineage in a one-shot breeding

environment is not coupled with male-male aggression. Given the diversity of animal phenotypes my hunch would be that such cases exist. Extremely short-lived insects such as mayflies, or in particular butterflies and moths such as the Emperor Gum-Moth, who have a very short breeding season in their life cycles, seem to have a one-shot breeding environment and (so far as I am aware) do not typically engage in male-male violence. There is a difference between having one breeding season and one breeding opportunity, of course. The point is that sometimes (perhaps frequently), we will find counterexamples to adaptive models. If we discover a disanalogy, then, what are we to make of the hypothesis? If we find a lineage with a one-shot breeding environment where males are meek, does this falsify Judson's hypothesis? Not necessarily. A commitment to biological externalism does not entail a commitment to Natural Selection optimizing, and it does not entail a commitment to Natural Selection's path being non-contingent. Just because it happens to be the case that a particular solution has not arisen in a lineage, this does not mean that this solution is not typically arrived at. However, the number of 'falsifying' examples, and the level of similarity between them and our target system, are important criterion for judging the level of threat counterexamples pose to a theory. If there are many examples, or if those examples are particularly telling (they are importantly similar), then we should be concerned about the theory.

As analogies can act as evidence for an externalist, adaptive model, so also can our confidence in externalism affect our confidence in analogous inference. If we think that Natural Selection's causal force reaches far and wide, we will be more ready to accept an analogous inference relying on that model. If we retrodicted the male behaviour of some extinct species of fish which lived in transient pools we might claim that they were violent based on our observations of Annual Fish (as well as Fig-wasps and Gladiator Frogs). This inference is only justified if the causal thesis of externalism is the case, if it is a robust-process that is information preserving enough to warrant projection into the evolutionary past.

So the epistemic warrant of analogous inferences is gained via the robust-process of Natural Selection. To judge the strength of this warrant, then, we must examine whether the causal thesis of externalism is true. It is here that the problem of causal depth emerges.

4.2 The Problem of Causal Depth

The problem of causal depth for analogy is due to noise from developmental processes interfering with the signal from Natural Selection. A problem of causal depth occurs when the process which underlies a particular inference is information-destroying to the point that we lack epistemic warrant to choose between competing hypotheses. Natural selection is constrained by the process of development. These constraints may make Natural Selection too information-destroying to ground analogous inferences. If this is the case, then analogies between lineages are not projectible onto other lineages. We could not use them for inductive inferences. If we take the Developmentalist criticism of Adaptationism seriously, then we should question whether analogous inferences have epistemic warrant.

This section is a discussion of constraints upon Natural Selection. Some constraints do not affect Natural Selection's 'signal', its projectibility, but others do. In particular, I think that developmental constraints cause significant noise. I will discuss non-developmental constraints and suggest that are not sufficient to cause a problem of causal depth. This will set me up to argue for the following two claims. First, the potentiality of a developmental system can affect the signal from Natural Selection, causing a problem of causal depth for an analogous inference. Second, it is typically the case that developmental systems erase this signal.

The discussion of constraints which follows is not intended to be exhaustive and aims only to identify the kind of constraint which is most

important for the problem of causal depth²¹. A constraint upon Natural Selection is anything which relativizes the adaptive solutions it reaches. As Roger Sansom (2003) has pointed out, constraints upon selection are in fact necessary for its explanatory potency. What counts as optimal must at least be relative to the environment in question. I want to identify those constraints which erase the historical signal from selection and undermine inferences reliant upon analogy.

Some constraints are fairly innocuous. For Darwin, Natural Selection did not reach global optima, but one localized in reference to the competitiveness of other individuals in a population. “Natural Selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it has to struggle for existence... Natural Selection will not produce absolute perfection (Darwin 2008 (1859) pp 235).” ‘Perfection’ is relative to the fitness of those other individuals competing in a population.

This constraint is accepted (if underemphasized) by modern Adaptationists (Dawkins 1996, Dennett 1995), as well as others. Because Natural Selection can only move traits towards increased fitness, if a trait must decrease in fitness in order to reach some higher optima, then that optima cannot be reached. In other words, if a ‘fitness valley’ exists between their current optima and a higher one, that higher one is inaccessible. Perhaps if all fig-wasps became pacifists the overall fitness of each individual fig-wasp would increase. But because any move towards pacifism on the part of an individual wasp results in a decrease in fitness, general pacifism cannot be reached. Another constraint is trade-offs between various traits within an organism. An increase in fig-wasp size might result

²¹ There are various ways of dividing up constraints – Gould distinguishes between phylogenetic contingencies (developmental history) and formal structural rules. He claims that what counts as a constraint is relative to the explanatory programme. Others may take a more objective approach. My discussion here is neutral to this debate, which is nicely arbitrated at the opening of Sansom 2003.

in more success in combat, but could have negative factors as well. Perhaps they would be less efficient at mating, for instance.

If these constraints affect the signal from Natural Selection, they do so in a similar way as Sober's 'bowl' example: they are due to the nature of Natural Selection itself. I do not think they are particularly troubling here. It is a commitment to externalism, that Natural Selection is the most potent force in the evolution of phenotype, which grants epistemic warrant to analogous inference. And externalism is not challenged by these examples. It is now time to make the first claim: Developmental processes can create a problem of causal depth for analogies.

A developmental constraint consists of information about what a particular developmental system can and (more importantly) cannot do. It constrains selection by tying possible design space to the potentiality of a particular developmental system. These constraints are, in Sansom's terms "... abstractions from the causal processes of development... (Sansom 2003 pp504)" They constitute a separate robust-process from selection.

Developmental constraints could affect the use of analogy because when we claim that two species are analogous and use them to make comparative inferences, we do it against an assumption that the two lineages have the same potentiality. For instance, if we wish to reconstruct the hunting behaviour of an extinct hominid we may want to use an analogue. We could use a pack-hunter, say wolves (as suggested in Sayers & Lovejoy 2008). For the wolf and our target species to be analogous, they must have developed the same adaptation in response to the same selective environment. For this to be the case, however, both lineages must have similar developmental options open to them: selection must have the stronger effect on phenotype than phylogenetic history.

Let us go back to inferring male-male violence in an extinct species of fish. Because we had reason to believe that this fish lived in a one-shot breeding environment and because we have analogous examples of male-male violence given that environment (Annual fish, gladiator frogs, fig-

wasps) we inferred that this extinct fish exhibited male-male violence. But what if the developmental system of the fish had interfered with Natural Selection? Maybe male-male competition was simply not in the potentiality of that system. Or alternatively some other evolutionary route was more likely given the developmental system. Perhaps the lineage evolved towards some different fitness peak because of its developmental potential. If this was the case then for this particular example we cannot project our selective model onto the target system. So, even if we are correct in our adaptive explanations of Annual fish, gladiator frogs and fig-wasps, because Natural Selection's path is constrained by the developmental system of the fish in question, we cannot then claim that our model holds true for it.

So, it is possible for a developmental system to constrain Natural Selection in such a way that some analogous inferences lack epistemic warrant. In these cases Natural Selection lacks the causal depth to affect phenotype. This does not undermine the causal thesis of externalism – externalism not holding true in particular cases is not enough to claim that it is false generally. The adaptive model can be right, but not applicable in this particular case. To do this we need to argue for the second claim of this section: development's constraint of Natural Selection is typically the case.

If internalism is true, that developmental resources have a stronger causal role in the shaping of phenotype than environmental pressures, then we have a generalized problem of causal depth. We are unjustified in assuming that an externalist hypothesis in one lineage will hold true in another. As we shall see in the next few chapters, different evidence will be required to prop up these inferences.

Paul Griffiths (particularly 1994) has argued against the use of adaptive categories in taxonomy on the grounds that, generally speaking, phylogenetic history is a much stronger force in shaping phenotype than Natural Selection. His argument could be summarized as a claim that the causal thesis of internalism is true, and so functional categories (part of the explanatory project of externalism) are inappropriate for taxonomy. I take it

that the purpose of taxonomy (at least in cladistics) is to represent the real evolutionary relationships between lineages. A 'taxonomy' which uses functional (adaptive) categories allows for cross-species generalizations. But these generalizations, Griffiths claims, are not robust. A cladistic taxonomy has more explanatory potency than a functional one. Natural Selection's causal efficacy is shallow.

Griffiths' argument that phylogenetic history is a much stronger force on phenotype than selection is made largely by exemplar. "It is a truism in comparative biology that similarities due to analogy (shared adaptive function) are 'shallow'. The deeper you dig the more things diverge. Bat wings and bird wings have similar aerodynamic properties but their structure diverges radically, despite their deep homology as tetrapod limbs (Griffiths 2007b, pg 216)."

Another striking example he uses (Griffiths 1994) is to compare two (relatively?) closely related species who occupy the same niche. If externalism is true, and selection is largely unaffected by phylogenetic history, then we should expect lineages in the same niche to share similar phenotypes. There are two exemplars he gives for the niche 'Top-Rank Fresh-Water Predator.' One is the crocodile, the other the anaconda. It is difficult to find resemblance-relations between these two lineages which are best explained in terms of adaptation. Their reptilian features are homologies, not analogies. According to Griffiths, we will find these discrepancies more often than not. This kind of example suggest that Natural Selection is importantly constrained by development, and moreover that that phylogenetic history has more influence over phenotype than selection. It shows that we cannot simply assume that Natural Selection will reach predictable optima.

These examples are telling, but inconclusive. I can see no way of claiming that, in principle, Natural Selection is shallow (this point is expanded below). However, as we examine these examples a case builds: typically, phylogenetic history tells us much more about a particular lineage

than niche. Developmental processes (most likely) do constrain the options open to Natural Selection enough to undermine its explanatory potency for questions of biological form. The causal thesis of externalism is (mostly) false.

I have focused on a broad question: what explains phenotypic form overall. As we have seen, adaptive hypotheses are usually about the function of a particular trait or suite of traits. So even if adaptation is a bad explanation for overall form, it does not follow that it is a bad explanation for a particular trait. So these considerations do not overly affect adaptive hypotheses (although they reduce the scope of externalism as an explanatory project). They do, however, affect analogous inferences. If Natural Selection's causal efficacy is shallow, then we cannot assume that what is true about the relationship between one lineage and its selective environment will be true of another. I am unwarranted in projecting from the behaviour of a fig-wasp to an extinct fish based on the analogous similarities between them. If this line of thought is right, when contrasting two competing hypotheses about the behaviour of the fish, analogies have a minimal role in corroboration. Much of the remainder of this thesis aims to show the conditions required to overcome this.

So the problem of Causal Depth can be expressed. We cannot readily grant epistemic warrant to inferences reliant on analogy because Natural Selection is too information-destroying a process. The influence of phylogenetic history overrides that of selective history. Before moving on to the next chapter, there is a last point I want to make about the problem of causal depth

The problem of causal depth is an empirical problem, not a conceptual one. We might think that analogies are shallow by their very nature. The similarity between analogues is functional, and therefore (we might think) more abstract than the similarities between homologues. If there is some trade-off between abstractness and specificity (presumably due to functionality or abstractness maps onto 'generality' in some sense), then

analogues have a grain problem due to their functional nature.

I think this kind of approach is wrong-headed. At the end of the second chapter I discussed the nature of the functional similarity between analogues. There I committed to Lycan's account of continuity between function and physicality. As we saw, functional and physical description could be either homologous or analogous. If this is the case, then analogies cannot have a grain problem due to their functionality (or, at least, that functional homologies have the same problem).

Another way of putting this point, I think, is to reemphasize that parallelisms can be as similar as homologies. If this is the case, then our explanatory inference that a particular resemblance-relation is homologous, leads us to cast the similarity in terms of physical (phylogenetic) continuity. If we infer an analogy, then we cast the similarity in terms of selective function. But that analogies are shallow is a fact of the matter; there is nothing necessary about analogies which leads to the problem of causal depth. So the problem of causal depth lies not with analogies themselves, but with the fact of their shallowness.

As such, one method to refute Griffiths, Gould and others would be to find examples of analogies where Natural Selection's effect is deep. This is not my approach. The question I aim to answer in the next three chapters is: given that analogous similarities are shallow, that there is a problem of causal depth, under what conditions can analogies remain useful to us?

Before turning to possible solutions, I want to bring into focus a particular case where I think the use of analogies would be most helpful: outlier lineages. This is the topic of the next chapter.

5. Outlier Lineages

This chapter sets the task for chapters 6 and 7. It describes an area where analogous inferences have obvious application: Outlier lineages.

In the last chapter I showed that the causal-thesis of Adaptation ought to be considered generally false (although it is true in some particular cases). As Adaptationism is necessary to grant epistemic warrant for analogous inferences, this undermines the use of convergences to construct adaptive models. I am unable (it seems) to project an adaptive explanation from one lineage to a target lineage.

In the first part of this chapter I will outline an explanatory target that analogies would be very helpful for. These are *outlier lineages*, lineages which are phenotypically isolated from their homologues. The use of homology is impoverished in the explanation of outliers, and I shall spend some time explaining this. I will then sketch a framework for the explanation of outlier lineages, which I will call an *evolutionary narrative*. An evolutionary narrative is an externalist, actual sequence explanation which hypothesizes the adaptive history of a particular trait or suite of traits belonging to an outlier lineage.

Before analysing the purported solutions to the problem of causal depth, I want to bring into focus the kind of questions analogies can help answer.

There is a kind of evolutionary question which analogies can help answer. These are explanations about the evolution of outlier lineages. An outlier lineage is phenotypically isolated, which limits our ability to use homology to reconstruct its evolution. I will use these limits on homology to set a particular role for that class of information in the retrodiction of outlier lineages.

With this in hand I will outline a framework for retrodicting the

evolutionary histories of outlier lineages – we need to construct an evolutionary narrative. There are two pieces of information required, one phylogenetic and the other adaptive. We need to know the initial conditions of the lineage, what state they evolved *from*. We then need to refer to an adaptive model which links the initial state to the final state.

I will ultimately argue that homology and analogy have very different inferential uses. Homology can inform the initial conditions and analogy the adaptive model. This division of labour is central to my solution to the problem of causal depth.

5.1 **What is an outlier lineage?**

In this section I will explain what I mean by outlier lineages and go over some inferential issues they pose. This will allow me to explain the uses of homology and analogy in such cases.

An outlier lineage has phenotypically departed from its relatives. Some of the planet's most successful lineages have not shifted from their basic design for millions of years. By contrast, some lineages have shot down unexpected routes through design space, becoming markedly different from their conservative cousins.

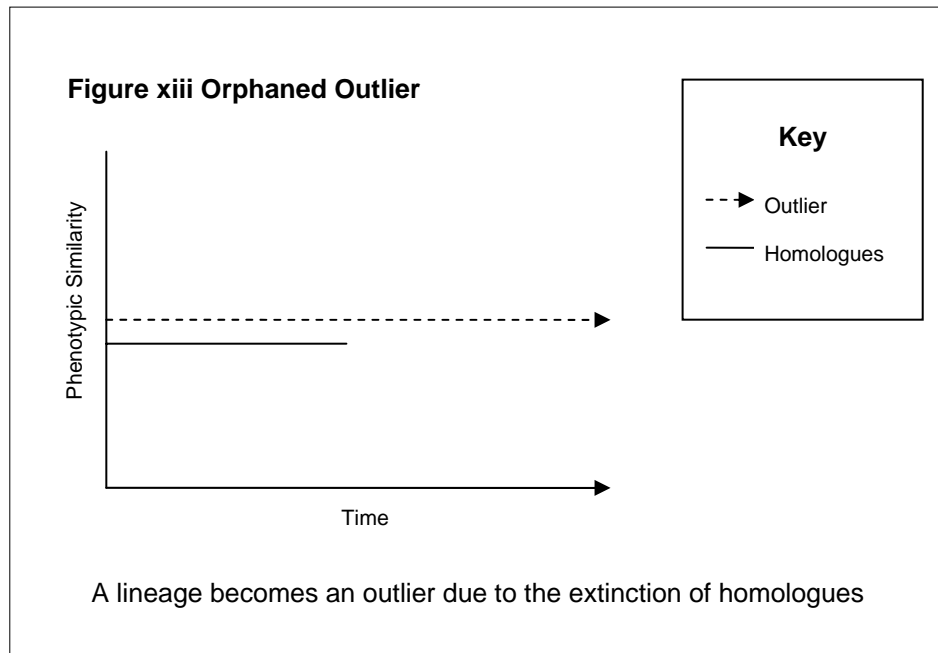
To count as an outlier lineage, a lineage must be phenotypically isolated. If a lineage has outlier *traits*, which are traits which are present in the target, but not in any close relatives, then it is an outlier lineage.

Pressure can be put on the distinction between an outlier lineage, and a mere variant. For instance, a particular species of Finch which happens to have a longer beak others does not count as an outlier. In such cases our inferential approach to explaining the difference is not the same as in more phenotypically isolated cases. For the Finch, analogies are not needed to explain the evolutionary difference. We instead rely on a 'longitudinal study' of the lineage and its relatives. For instance, if beak-size variation was modelled by studying beak-length versus various dimensions of possible selected effect (available food, population and so on), then we could

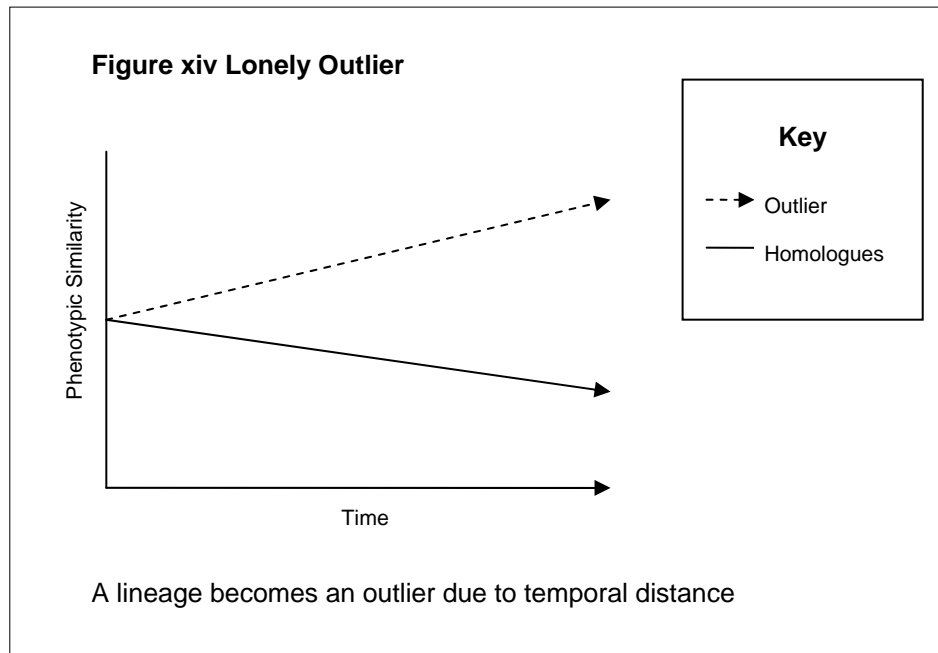
extrapolate any regularities discovered onto our target. This longitudinal approach gives a micro-evolutionary explanation (see Grant & Grant 2006 for a ‘longitudinal’ study Darwin’s Finches beaks). To count as an outlier, an explanation of the outlier traits must not be amenable to these real-time studies. The phenotypic isolation must be deep and complex.

There are several ways a lineage could become an outlier. If a lineage’s relatives have died off it may be left with unique traits. This is an *orphaned* outlier²². The Nautilus clade consists of six species across two genera. Fossils suggest their basic form has remained unchanged for 500 million years. They are the only cephalopod to have a coiled shell, or any hard external casing at all. The Ammonite relatives of the Nautilus, which shared this similarity, went extinct at the K-T extinction event (Dawkins 2004, pg 394). The Nautilus Clade, then, is an outlier in virtue of the ammonite extinction.

²² A related idea is David Jablonki’s concept of a *Dead Clade Walking* (2002). There is a tendency for certain clades, having survived mass extinction events, to become extinct in the aftermath. Survivors from such clades may become orphaned outliers, or if the temporal distance is long enough, lonely outliers (such as the tuatara). An interesting question is why, if Dead Clades are fairly robust phenomena, some groups occasionally manage to survive given the extinction of the remainder of their clade. What, for instance, explains the survival of the tuatara?



If a lineage has travelled a distinctive phylogenetic path for long enough, it sometimes evolves traits that are divergent from its relatives. This is a *lonely* outlier. The two species of Tuatara, for instance, have followed a separate evolutionary path from any other reptile for at least 200 million years. Over time, differences have accrued between them and their relatives. Their parietal eye, for instance, has either been lost in the main reptile group or evolved independently in the clade after the split. So the tuatara is an outlier lineage in virtue of the temporal distance between itself and its cousins. The platypus and echidna, as well, are outliers in virtue of the deep phylogenetic distance between them and other extant mammals.

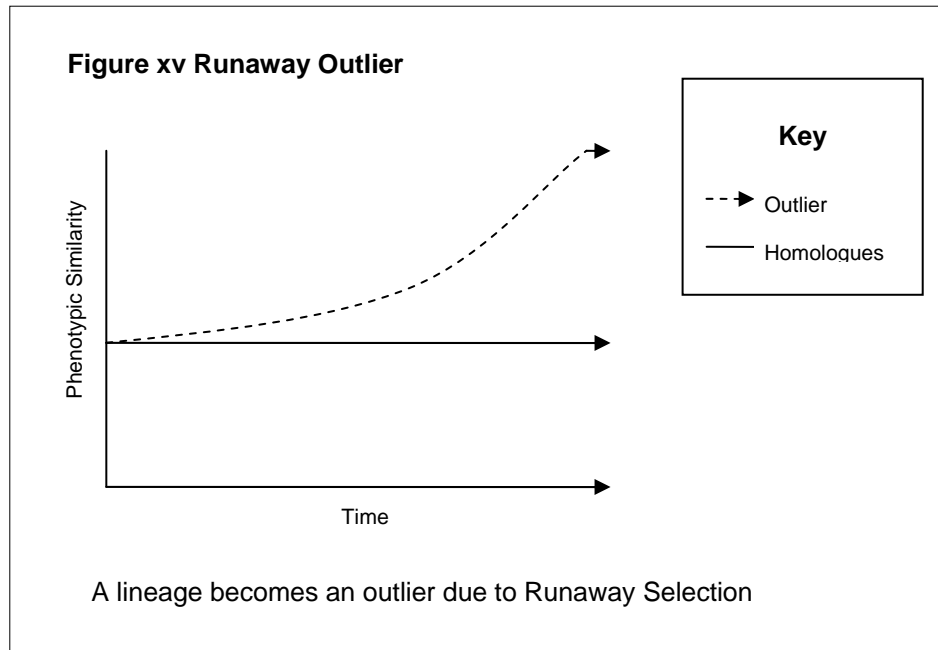


Sometimes the difference between lonely or orphaned outliers is indistinct. If an outlier lineage has undergone minor phenotypic change in its life history, and is unique due to the extinction of cousins, then it is lonely. If it has undergone significant phenotypic drift, then it could be a *lonely orphan*.

Mere temporal distance or phylogenetic isolation alone is not enough to count as an outlier. The clades represented by the two genera of *Nautilus* have a common ancestor in the deep past, so they have plenty of temporal distance between them. But, in the context of the *Nautilus* clade, they are not outliers because the lineages have not diverged enough. A lineage is an outlier due to phenotypic distance, not temporal. For the *Nautilus* clade, the phenotypic distance between it and its closest relatives is explained by temporal distance and the extinction of the clade's relatives.

Finally, a group may become an outlier because of runaway selection, typically due to entering a new niche. These are *runaway* outliers. The cetacean lineage (whales, dolphins and porpoises) is nestled within the artiodactyls (even-toed ungulates). Their closest extant relative is the Hippopotamus (the 'hippo' hypothesis: Dawkins 2004 pp 202-210,

Marino et al 2007)! The obvious contender for explaining the enormous difference between a dolphin and a hippopotamus is adaptation to a salt-water niche. Examining the hippopotamus cannot tell us how the cetaceans evolved from land-living hoofed mammals to sea predators; it is unclear whether we should consider the most recent ancestor of the two lineages ‘hippo-like’ or not. The distance is just too far.



So, a lineage may become an outlier due to the extinction of homologues (becoming orphaned), or temporal distance (becoming lonely), or due to rapid phenotypic change (running away). All result in phenotypic isolation, which, as we shall see, massively limits the use of homology. Before discussing these limits, I want to discuss the hominid lineage as an outlier, as I will be using our ancestry as a case study throughout this chapter and the next two.

Homo-sapiens is an outlier lineage. Not only are we phylogenetically isolated but we have many apparently unique, ubiquitous traits. These range from physical adaptations such as bipedalism (Sayers & Lovejoy 2008) to psychological and cultural adaptations like language and abstract thought. We are, then outliers on two counts. Our lineage is characterized by rapid

evolutionary change leading to a suite of traits not present in our homologues. Also, all other members of the hominid clade have become extinct. In short, we are *runaway orphans*.

Some research programmes (most notably Evolutionary Psychology) seek to explain such unique traits in Adaptationist terms (Workman & Reader 2004, Pinker 1997, Barkow et al 1992). An adaptive explanation is appropriate for these traits - their high cost and specific design suggest are diagnostic of adaptations. However, their novelty impoverishes the application of comparisons with homologues.

Jonathon Kaplan (2002) has argued that due to the phenotypic isolation of hominid traits, our evolutionary history is out of inferential reach for comparisons with other lineages. In order for a lineage to give good evidence about the evolutionary history of a trait, we must be able to calculate the fitness consequences of that trait. With Finches, repeated 'longitudinal' observations allowed us to find the fitness consequence for beak-length. If there are no available homologues to make such a calculation, then the information (through this route at least) is inaccessible.

Kaplan appears to either ignore analogy or conflate it with homology. As we shall see in the next section, given the nature of outlier lineages, it is trivial to point out that homology cannot provide evidence for fitness consequences. He doesn't consider non-homologous similarities between humans and other lineages. Independently evolved resemblance-relations, if they exist, would constitute better evidence for adaptive hypotheses about hominid evolution than homologous similarities (see below). So we should search for analogies as well. This is not to suggest that all of our traits have available analogues. Language, for instance, might be a truly unique trait. If there are no analogues or homologues for a trait, then comparative data cannot shed light on adaptive models.

So far we have learnt what it is to be an outlier lineage. A lineage counts as an outlier just in case it is phenotypically isolated and that isolation is deep (not amenable to longitudinal study). The hominid lineage is an

example of this. With the focus is firmly on our own lineage, I want to make some points about the use and limitations of homology before going on to exposit the explanatory structure which ought to be applied to outlier lineages.

5.2 Jolly's Paradox and the Limits of Homology

When our explanatory target is the emergence of novel features in an outlier lineage, the use of homology is especially limited. This is in part due to the nature of outlier lineages - the target trait will not be present in homologues. But we also must be careful to demarcate the vital but different roles that analogues and homologues play. A discussion of 'Jolly's Paradox' will lead me into the next section where I will argue for a division of labour between them.

Some properties of outlier lineages weaken the use of homology. To see why, we need to consider the epistemic basis for homologous inferences I discussed in chapter 3.

Homology has varied uses in evolutionary biology. It can be a data point for the reconstruction of ancestral phenotypes; to help calibrate a molecular clock; to test adaptive hypotheses; to set the phyletic relationships between lineages. My interest is in the use of homology to project traits from one lineage to another, thus telling us about the phenotypes of their ancestors, the phenotypes of extant relatives and helping to construct and test adaptive hypotheses.

I have previously argued that homologous inferences (in the cases I am interested in) gain warrant from developmental entrenchment and cladistic parsimony. There are three reasons that homologous inferences are typically weakened in outlier lineages. First, although outlier lineages are not characterized by temporal distance they are frequently phylogenetically (as well as phenotypically) isolated. Second, if some traits have undergone rapid evolutionary change, this suggests that the trait is evolutionary labile. And temporal distance and trait lability weaken developmental entrenchment. Third, an outlier lineage will usually lack data points for clade construction.

This weakens cladistic parsimony. I will take each point in turn.

If there is temporal distance between a lineage and its homologues, this can weaken homologous inferences. In chapter 3 I discussed the use of the Googly-eyed Glass Squid to model the Colossal Squid. Our basis for assuming they shared behaviour was the minimal phylogenetic space between them. Because phenotype is typically preserved across generations, traits can be projected from a homologue to a target across small phylogenetic distances. Imagine now that the temporal distance between the two species was extended. The longer they have diverged – the lonelier the lineages – the higher the chance that any particular trait would have changed (unless there is very strong stabilising selection acting on them). So if the two squid lineages had diverged enough, we would have little basis to claim any particular similarity between them. Outlier lineages, particularly lonely and orphaned ones, are typically temporally distant from their homologues, and so developmental entrenchment might not provide epistemic warrant for homologous inferences.

If a trait has evolved rapidly in a lineage then this trait is probably labile in the clade in question. In primates kin-structures appear to be particularly labile. Across the group there are many different arrangements, and close relationship is not a good guide for what particular structure a lineage will have. This suggests that it is ‘easy’ for a primate to change its social structure, at least over evolutionary time. A runaway outlier has recently undergone a set of deep, complex evolutionary changes. If an outlier is a runaway, then, there is a good chance that their outlier traits will be labile. If this is the case, then developmental entrenchment cannot guide inferences about the traits these lineages held in the past (kin-structure in primates is discussed in more detail next chapter).

An outlier sometimes lacks data points for cladistic analysis. Compare an impoverished clade to those which systematists prefer. *Hominidae*, the clade which consists of the Great Apes and Humans, has perhaps eleven species spread over roughly thirteen millions years (Kaplan 2002). Compare this to

the Cichlid fishes in Lake Victoria, who evolved roughly 450 species in 100,000 years (Dawkins 2004); or with the lungfish discussed in Schultze's work (see chapter 2), which have many species spread across three continents (Schultze 1994). The difference in sheer bulk is striking. If our data only consists of a few species then the probability of the most parsimonious arrangement being correct will decrease.

So the epistemic warrant of homologous inference is weakened in outlier cases. I will now turn to a different point about homology which I will make in the context of using homologues to inform human evolution. If we are asking an adaptive question about an outlier trait homology has a particular role to play. It is very important that this role is clearly delineated.

There is much debate about use of the *Pan* clade, Chimpanzees and Bonobos, to model hominid evolution. Some emphasize the similarities between us and *Pan*, claiming that our outlier traits are phylogenetically continuous. For instance, Frans De Waal (amongst many others) has claimed that human morality is rooted in *Pan* cooperative behaviour (De Waal 2006, see also Katz 2000); Bernard Chapais and others have claimed that human kinship structures can be traced from those of *Pan* (Chapais 2008, Rodseth & Shannon 2006); and Darwin believed that an understanding of primates would revolutionise our understanding of human nature, which he demonstrated using homologues between human and chimp emotional expression (Sterelny & Griffiths 1999). What these theories have in common is the denial of a discontinuity between human and chimp. We do not need to look at any information from outside the *Pan-Homo* clade, or maybe outside of *Hominidae*, for answers to questions about human adaptations. Like the long-beaked finch from the previous section, we can simply extrapolate the adaptive model for our evolutionary story from observations of homologues.

For some traits this is the case (emotional expression is homologous between hominids and other primates) but there is reason for worry which is interestingly (but perhaps misleadingly) expressed in 'Jolly's Paradox'. My

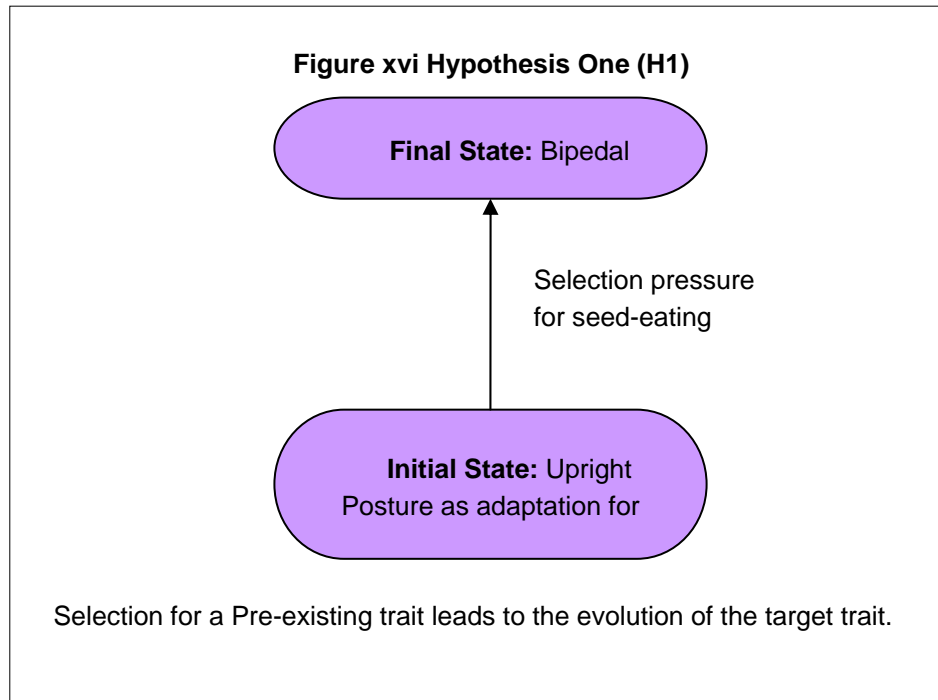
aim is to use a discussion of the ‘paradox’ to illustrate the role which homology has to play, and to lead into a general story about the retrodiction of outlier lineages.

Sayers & Lovejoy (2008) argue forcefully against the use of *Pan* as a model for hominid evolution. They rightly take issue with the use of chimpanzees and bonobos as analogues. In some cases they argue that traits which are taken as analogous between primates and hominids are not actually analogous. For example they think (and argue in exhaustive detail) that the regular taking of an upright posture in primates is not an analogue of bipedality as the physiological criteria for bipedality is significantly divergent from typical primate physiology. They also argue that there is a double standard between primatology and animal behavioural studies. A primatologist, they claim, is much quicker to assert that a particular behaviour is cultural or learned than a scientist working on the behaviour of other animals.

Their most interesting argument is the claim that an increase in similarity between chimp and human makes the job of explaining unique hominid traits harder. This is ‘Jolly’s Paradox’. Discussing tool-use Sayers & Lovejoy have this to say: “... the more chimpanzees are shown to be skilled in making tools, the less effective their tool-making becomes as a criterion for the earliest human behaviour. (pp89).” Why justifies this claim? If they are right, then it seems to follow that the more similar an ancestor is to our target the harder our explanatory task. I will examine their position in more detail in reference to bipedality.

Clifford Jolly has used Baboons taking an upright stance to construct a model of the evolution of bipedality (Jolly 1970). Baboons typically adopt an upright stance in order to collect and eat seeds. Jolly suggested that selection for uprightness as an adaptation for seed-eating could have led to bipedality in the hominid lineage. It is not clear whether he means this to be a homologous inference, where our common ancestor with Baboons took an upright stance for this purpose, or an analogous inference where our

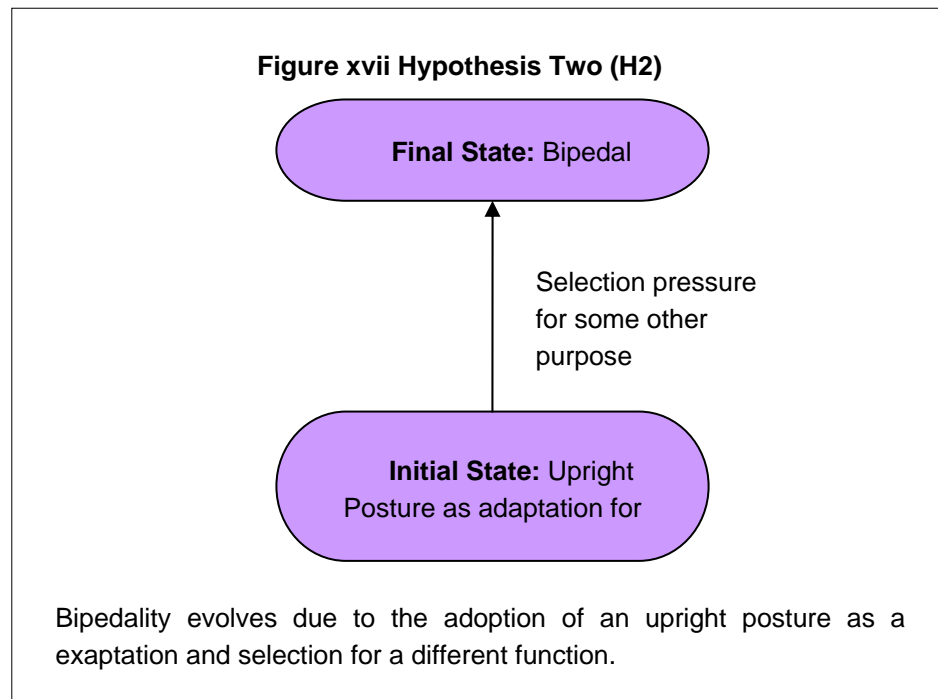
ancestors evolved an upright stance in parallel with Baboons. Either way, his idea can be expressed as a hypothesis (H1) which takes an adaptation from the ancestral state and supposes that selection for that adaptation led to the explanatory target.



Sayers & Lovejoy argue that if the upright stance is used for a purpose successfully in primates, then it doesn't make sense for selection to favour selection for bipedality for that purpose. That baboons regularly take an upright stance when eating seeds, they claim, shows that bipedality is *not* an adaptation for seed-eating. Baboons are well adapted for seed-eating. Why would selection favour an evolutionary change to a body design which seems to come at such cost, when the current arrangement is sufficient? Bipedal hominids lose arboreal access and quadrupedal speed. "The more it can be demonstrated that primates can effectively practice it [upright-stance], the less probable it becomes as an explanation for the *singularity* of compulsory hominid bipedality (Sayers & Lovejoy 2008)."

So for Sayers & Lovejoy H1 is not a good hypothesis for the evolution of bipedality. They think a theory which postulates a different selection

pressure is necessary. So, even if hominids did take an upright stance in the evolutionary past, our explanation needs to postulate a change in the selective environment. Uprightness is, at best, an exaptation.



Their case is overstated. First, it is not clear that Jolly actually means that uprightness is anything other than an exaptation. This is clearly the most reasonable way of reading his hypothesis. Second, it is not necessarily true that selection for bipedality requires selection pressure for a different purpose. If there is some trade-off between the fitness inferred from seed-eating and the fitness inferred from a quadrupedal gait, then the mitigation of that trade-off could allow selection to favour bipedality. Perhaps, for instance, the shift from forests to plains removed selective pressure on arboreal adaptations. It could just be the case that selection for seed-eating (assuming that bipedality is a more efficient means of doing so) was stronger in the hominid lineage than in baboons.

Having said this, they are on to something important. It is not that increased similarity leads to more difficult explanations. The important point is that if we are to explain why hominids are different to other

primates, we need to draw on differences between the past selective environments of hominids and other primates. If both hominids and Baboons lived in the same selective environment, then why is it that hominids evolved bipedality and Baboons did not?

So Sayers & Lovejoy's point about Jolly's Paradox is best understood as emphasizing the need for a *difference-maker* in adaptive explanations. Possible difference-makers are divergences between a lineage and its homologues. What is the trait, developmental resource, or environmental variable which drove the lineages down divergent paths? The explanatory target for outlier lineages are the divergences between the lineage and its homologues. By using the same lineages as both homologues and as analogues, therefore, the difference maker is easily obscured.

For the retrodiction of some outliers, the difference-maker will be less important. If a lineage is an outlier due to temporal distance, then it may not be the case that its outlier traits can be explained solely, or even at all, in reference to external explanation. If a lineage has evolved due to drift or some other non-selective process, the differences in environment are not sufficient to explain the phenotype. It is in adaptive, external explanations that we want to identify difference makers. So for lonely outliers, and some orphans, the difference-maker is less important because an externalist explanation is less appropriate. But when we are considering cases where lineages have become outliers due to homologue extinction or rapid evolutionary change this is less likely.

So, to focus my aim here. I am concerned with the proper strategy for retrodicting outlier lineages of the type which *Homo-sapiens* exemplify. These lineages are runaways, phenotypically isolated because in the relatively recent past there has been rapid evolutionary change. We have evolved unique traits (presumably adaptations) due to a particular set of selective environments. Also, these lineages are orphaned; they lack close homologues. Because all other hominids are extinct, we cannot (directly) observe them.

One method of finding a difference maker is to examine contrastive information between the outlier and its homologues. Any comparative (homologous) information does not warrant an adaptive explanation for the emergence of that trait (naturally, we may want a selective explanation for its maintenance). All of *Hominidae*, including humans, are warm blooded. So what? Our explanatory target for the emergence of warm-bloodedness is in the distant past, long before primates evolved. But, contrasts between *Homo-sapiens* and its homologues do possibly require adaptive explanation. We are uniquely adapted to compulsory upright walking. The bipedal question asks what was different about past Hominid selective environments which meant we evolved an upright posture when *Pan* did not. The explanatory target is this divergence in trait. The difference-maker will be some quality (most likely in the selective environment) which Hominids were exposed to, and *Pan* were not.

Sayers & Lovejoy miss the vital role which homology does play. Homologous inferences are the best means we have of setting the *initial conditions*. Even with a strong fossil record, cladistic methods are still required to set the evolutionary relationships between the extinct lineages. For instance, that many primates habitually take an upright stance suggests that our non-bipedal ancestors also habitually took an upright stance. This does not tell us that this habit is an exaptation for obligatory bipedalism (in fact its apparent ubiquity suggests otherwise), but nonetheless our initial conditions will include this trait. Getting a good picture of the original state is absolutely necessary.

I am now in a position to outline the use of homology for outlier lineages. *Comparative* information can inform the initial state – the ancestor who evolved into our target system. *Contrastive* information hypothesizes difference-makers for our adaptive explanation. Jolly's Paradox is a pessimistic take on the relationship between homologue and target. The higher the similarity between the target system and the homologues, the more in common the initial conditions are to the final conditions – and the more difficult the task of identifying difference makers. If Chimps are tool-

using, upright-stance taking, cultural-learning, hunting primates, why on earth did they not evolve into a species as apparently successful and varied as *Homo-sapiens*? In a sense Sayers & Lovejoy are right: the higher the similarity between the initial conditions and the final state, the more confounding the adaptive problem is.

With the role of homology exposited, I will explain the inferential structure applicable to runaway orphan outlier lineages.

5.3 Evolutionary Narratives

This section gives an account of the structure of an adaptive explanation for an outlier lineage. The model might be generalizable to all adaptive explanations but whether this is the case is not my concern here. It will set a clear division of labour for homologous and analogous information. Homologues set the initial state, analogues inform the adaptive model. I am interested in what I will call evolutionary narratives and will contrast this to Brett Calcott's notion of a lineage explanation (Calcott 2009).

What do we want from an explanation of an outlier lineage? If we want to know, say, why elephants have such prominent proboscises, what information are we asking for? We want an *evolutionary narrative*. A story which tells us how something which wasn't an elephant, evolved into something which is. We require an actual-sequence explanation – there is a fact of the matter about how some proto-elephant ('protophant') which lacked a trunk, evolved into an elephant. This narrative is our explanatory target.

What does an evolutionary narrative consist of, then? The narrative is a set of ordered changes in the lineage – the changes will either be in *phenotype* or *environment*. To keep with the fanciful elephant theme, let's say the story goes as follows. First, the protophant environment shifted from forested to grassland. Second, the protophant phenotype evolved a more efficient olfactory system. Third, the environment shifted due to an increased number of grazing animals. Finally, the protophants evolved proper elephant trunks. An evolutionary narrative is not just a temporal sequence,

however. This misses an important element. I still need to explain *why* the protophants evolved trunks.

To answer our question, the narrative must explain the *relation* between these four events in terms of adaptation. Perhaps the increase in grassland (event 1) caused a selective environment which favoured long-distance methods of finding food. The protophants evolved more efficient noses (event 2) for this purpose. As other animals moved into the grasslands (event 3) competition for food increased. This environment favoured ways of exploiting new food sources, which the evolution of the trunk (event 4) enabled the protophant to do. So in this toy example selection for efficient olfactory traits provided an exaptation for the evolution of trunks.

The relations between the events refer to some kind of robust-process (which could be expressed as an adaptive model). The claim that a shift into grasslands creates a selective environment which favours the evolution of an efficient sense of smell is based in a more general statement. Generally, a grassland environment (due to the greater distances, perhaps) selects for a more efficient sense of smell²³. As we shall see, these informal models ought to be informed by analogies.

So an evolutionary narrative consists of a set of shifts in phenotype or environment, and the adaptive relations between them. There are two tasks for the ‘evolutionary storyteller.’ We need to know about the events themselves – this is the actual-sequence explanation. And we need to know about the selective processes acting upon the lineage – this requires a robust-process explanation.

To clarify the notion of an evolutionary narrative, I want to contrast it with Calcott’s *lineage explanations* (Calcott 2009). One question we might be interested in when considering evolutionary change is how it is, mechanistically, that traits change over time. In the evolution of eyes, for

²³ I am not suggesting here that any of these claims are actually the case, if anything grassland would select for better eyesight. It is meant only as an example.

instance, we want to know how it is that a light-sensitive spot could evolve, in a step-by-step fashion, into a lens eye. What sequence of small shifts could make the idea that eyes have evolved plausible? This is a lineage explanation.

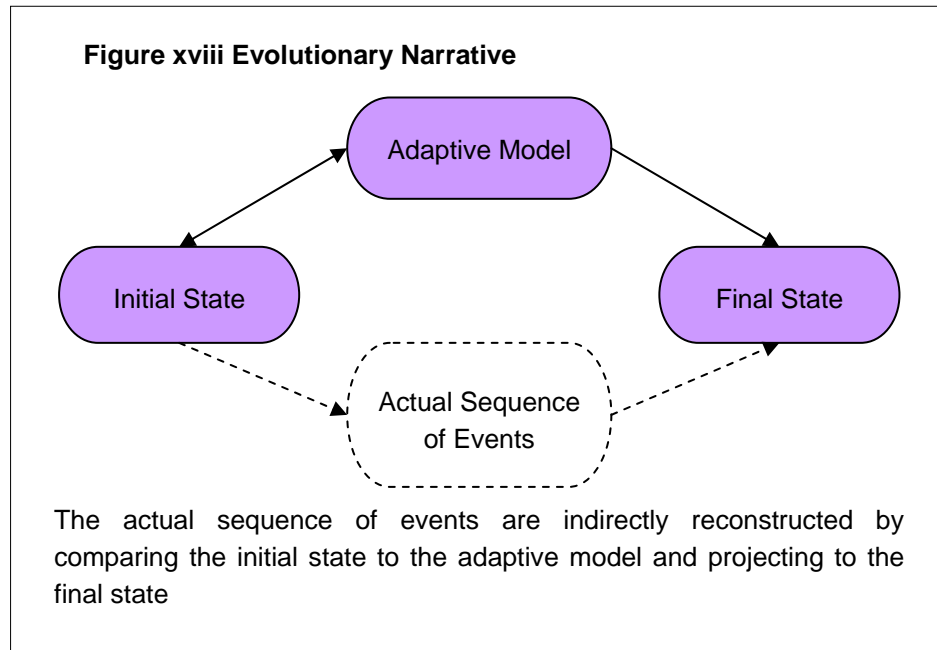
For Calcott, lineage explanations have two main requirements. They have a *continuity* requirement. Each successive stage must be only slightly altered. The shifts between stages cannot be large leaps – the evolution from a light-sensitive spot to a lens is a gradual process. They also have a *production* requirement. There are functional criteria the trait must meet at each stage of evolution. For instance, each successive stage of eye evolution must grant better eyesight (acuity or focus).

A lineage explanation of trunk evolution, then, would be an ordered sequence of mechanistic changes in nose design which shows how a normal mammalian nose might gradually evolve into a trunk. The main difference between this explanation and an evolutionary narrative is that an evolutionary narrative is (ideally anyway) firmly externalist. We identify the relations between shifts in environment and adaptations which lead to the evolution of trunks. Not the internal changes (given particular adaptive functions) which mechanistically explain the trait's evolution.

So while a lineage explanation is a quasi-internalist (insofar as the selective information is one directional in the production requirement), robust process explanation (it tells us about how trunks could evolve generally, not necessarily how they did evolve in protophants), an evolutionary narrative is firmly externalist and actual sequence. We want to know, in the actual case of elephant evolution, what shifts in environment and phenotype explain the selection of trunks.

An evolutionary narrative has something akin to Calcott's two requirements. The continuity requirement is nowhere near as stringent (as we do not need to explain evolutionary shifts mechanistically), but it is required that the differences in phenotype at each stage be causally linked to differences in selective environment. The production requirement is altered

as well. In a lineage explanation, the optimal production remains static (in the case of eye evolution, it is an increase in focus). In an evolutionary narrative, the production is two-directional. Successive phenotypes change the selective environment, just as differences in the selective environment drives changes in phenotype.



The three central parts of an evolutionary narrative (at least in a simplified sense) are the *initial state*, the *final state* and an *adaptive model*. Before explaining the roles of homology and analogy here, I need to say something about what constitutes the states, the model and how they relate. My account is simplified as it ignores the role of non-selective processes in evolution. Drift and developmental constraints can be an essential part of an evolutionary narrative. For the purpose of clarity I will ignore these to focus on an externalist model. Ideally, non-adaptive processes which have a role in the forming of phenotype would be incorporated into the adaptive model or initial state.

The original and final states (and any necessary states in between) consist of a set of variables. In the protophant example, for instance, the original state included variables such a forested environment and a small, inefficient

nose phenotype. The final state included a grassland environment and a trunk phenotype.

An adaptive model also consists of variables, but these will be a set of conditions for the evolution of a trait. These variables can be categorized into selective and developmental. So perhaps the evolution of trunks requires a highly competitive grassland environment (a selective variable) and a large, efficient olfactory system (a developmental variable). Given the right combination of selective and developmental factors, the trait will evolve.

Contrastive information between the initial state and the adaptive model sets difference-making variables. In my toy example, the initial state and the adaptive model share the developmental requirement of an efficient nose. They diverge on the selective requirement of higher food competition. So we would conclude that the difference making variable which drove protophant evolution towards trunks is the increase in population which caused an increase in competition for food.

With this in place, I can now state the division of labour between homology and analogy. Homology is useful in setting the original state, but is unhelpful for the adaptive model²⁴. Analogy may have a small but contentious role for the original state, but can be both inspirational and corroborative for the adaptive model.

What information could inform the original state? There are two sets of variables required, environmental information and phenotypic information. Many historical sciences can inform the initial state, paleobotany, paleoclimatology, and a host of other ‘paleos’, but I want to focus on homology. Any fossil remains, be it plant matter, fecal or animal, rely upon cladistical analysis to set the relationships to the target lineage. Although it a matter of great contention to claim any particular fossil lineage is actually

²⁴ This is focusing on *extant* homologues. In the hominid case extinct homologues have proven a very important stream of evidence in constructing the evolutionary narrative.

an ancestor of a target lineage (Sober 1988), homologous studies can give us good evidence of cousinship to the target in the same fashion as it does for living species. If there are no fossil remains, then homology can provide a picture of the initial conditions if there are enough homologues of the right relationship to grant warrant. For instance, in the hominid case extant relatives can inform us about our ancestors at the *Pan-Homo* split, approximately 6 million years ago, and further back – but not any closer to the present (see Suddendorf 2003 for an overview of homologous uses looking specifically at the Great Ape-Hominid case).

Analogues are limited in informing the initial state. As we saw in the last chapter, ‘Reverse Engineering’ is an Adaptationist method for inferring past adaptive environments from current adaptations (Griffiths 1996). Information about previous environments are part of the initial conditions. Perhaps an analogue could corroborate an adaptive hypothesis which claims that a particular selective environment causes a particular adaptation. But this is the kind of claim we rejected in the last chapter. Because adaptive forces are affected by historical stochasticity, we should be suspicious of historical inferences made on an adaptive basis. As we shall see in chapter 7, given enough corroborating evidence this kind of inference may be acceptable. But for now let the scepticism stand: analogues are little help in setting initial conditions.

Analogues can give us empirical traction on adaptive models. We have already seen how tenuous adaptive hypotheses are. The ‘natural experiments’ provided by other lineages independently evolving the same adaptations are the best method of corroboration that we have (although see the Coda for an attempt to extend what we mean by ‘analogue’).

Homology should not be used in the adaptive model (although see chapter 6). We seek to explain the traits which are not present in the

homologies. So homologies have no part in modelling²⁵ the conditions required for the trait in question to evolve (although insofar as they have informed the initial conditions, they are necessary for discovering difference-makers).

To close off this section, I want to provide a series of idealized steps involved in an evolutionary narrative

1. *Setting the Initial Conditions*: The previous phenotype and environment is inferred using a suite of historical inferences (importantly homology)
2. *Setting the Final State*: The final position is described, in complex situations there may be transitional states.
3. *Setting the Adaptive Model*: the variables required for the evolution of the trait in question are hypothesized. (analogues are very important for this, how they can be used in this context is the topic of the next to chapters)
4. *Hypothesizing the Difference-Maker*: contrastive information between the initial conditions and the adaptive model provides possible difference-making variables.
5. *Retrodiction of the Evolutionary Narrative*: hypothesize when, how and why the difference-maker/s arose in the lineage in question (to be corroborated by historical sciences)

These steps are idealized. History can be a very messy process and it would be awfully surprising if *any* evolutionary narrative fit this idealization. For complex, phylogenetically isolated traits there will frequently be several

²⁵ As an aside, some philosophers in science have discussed, and in fact defined, models in terms of a-priori construction (Odenbaugh forthcoming, Weisberg 2007, Godfrey-Smith 2006). For these philosophers, something is only a model if it is constructed *indirectly* without reference to actual-world systems. If they are right, then we should not think of what I am discussing as a ‘model’, as it is primarily empirical in its construction.

‘initial’ conditions, each with their own difference-makers and adaptive models. Even my protophant toy example involved extra steps than those given here. Nonetheless, this gives us an idea of the approach required for these retrodictions and will be central to my arguments for the remainder of the piece.

The next two chapters will consider two solutions to the problem of Causal Depth. The first emerges from what has been named the ‘Historical Turn’ (Griffiths 1996). Here we tie adaptive inferences to developmental processes. In the context of analogy we must constrain our possible catchment area of analogues to closely related species (something like this move is endorsed in Gould 2002, Sansom 2003, Powell 2007 as well as in Griffiths’ work). I will resist this solution and suggest instead that we do not need to constrain our catchment area as stringently as defenders of the Historical Turn prescribe.

6. Parallel Modelling

In this chapter, I discuss a possible to the problem of causal depth: ‘Parallel Modelling.’ We constrain our catchment area by developmental criteria. This way, only ‘parallel’ analogues count as data points. This gains epistemic warrant by ‘piggybacking’ the warrant granted to underlying developmental homologies.

A parallel model constructs an evolutionary narrative by providing an adaptive model which is constrained to a particular clade. The model will specify the relationship between phenotype and environment given a particular developmental tool-kit. So it might tell us what selective environment is required for the evolution of bipedality in great apes.

I do not disagree with the approach – in the appropriate circumstances. My argument next chapter is that we need not necessarily constrain our catchment area in the way prescribed by parallel modelling.

6.1 The Parallel Solution

The ‘Parallel Solution’ to the problem of causal depth claims that epistemic warrant can only be granted when projecting traits from an analogue to a target outlier lineage if those analogies are *parallel*. When we wish to use analogies in evolutionary narratives, therefore, we should restrict our catchment area to those lineages which are closely related to our target.

In his 1996 paper *The Historical Turn in the study of adaptation*, Paul Griffiths argued that adaptive hypotheses ought to incorporate phylogenetic history. Because history, as expressed in developmental resources, plays a large role in shaping phenotype (the causal-thesis of internalism is strong), an important part of an adaptation’s explanation is its phylogenetic history.

When using comparative data to test adaptive hypotheses, it is important

that we do not over-count confirmations. As Griffiths notes, it is the independent evolution events which count as data-points for the connection between environment and trait. If the data is homologous, it cannot explain the emergence of the trait.

Griffiths' position is not a rejection of the explanatory project of externalism. It is a modification of it. The claim should be read as emphasizing the role of developmental resources in the initial conditions. By contrasting adaptive models which incorporate historical factors we will create more robust theories.

From the Historical turn, a solution to the problem of causal depth arises. If we constrain our catchment area to groups united by a set of developmental resources, we can gain epistemic warrant for analogous inferences which take a relationship between environment and phenotype in one lineage and project the relationship onto a target outlier. Effectively, the noise created by phylogenetic history is removed. So, if we restrict our search to parallelisms as opposed to isolated convergences, our inferences will be warranted on both externalist and internalist grounds. To get a picture of the parallel solution, we need to look closer at what a parallelism is.

What is it to be parallel? I leaned heavily on this distinction in chapters 1 and 2, at the time giving a rough definition which I will stick with for now before questioning in the next chapter. Two traits are parallel just in case they are analogous (independently evolved), but utilize the same developmental resources. Gould (2002) gives an example of this.

The leg formation of *crustacea* is controlled by a group of Hox genes which are developmental homologies across the clade. A common crustacean trait is Maxillipedalism, the transformation of limbs originally for walking into eating apparatus. This has independently evolved numerous times, but "...always under control of the same developmental rule, presumably a pleisomorphic [synapomorphic] trait of the clade (Ibid, pp 1134)." So these are not merely cases of convergent evolution, but of

parallel evolution.

The developmental process which leads to Maxillipedalism gives a firm basis for analogous inferences. As Gould puts it, "... the value of parallelism becomes greatly increased by the operational basis thus granted to firm and testable explanations – by moving away from Adaptationist scenarios in the largely speculative mode, and towards morphogenetic rules with specifiable, even predictable, variations (Ibid pp 1132)." So, because we can predict and explain what is going on at a developmental level, and on homologous grounds are justified in extrapolating this information across all lineages with that developmental system, these analogies gain epistemic warrant.

Parallel analogies, then, 'piggy-back' epistemic warrant from underlying homologies. If the lineages in question have relevantly similar developmental tool-kits, then their contrasts will be caused by environmental factors. In effect, we 'control' our external explanation for internal noise. Our explanation incorporates both homologous and analogous information, and both count towards epistemic warrant.

Recall that the aim of analogous inference is to inform an adaptive model which can then be contrasted with the initial conditions. When using parallel analogies there is a particular structure to the model which I will sketch using two examples from work on hominid evolution. First, Chapais (2008), focuses on an underlying developmental cause to construct a kind of 'design-space' for primate kin-structures. Second, the relation between Teste size and sexual dimorphism in primates provides a similar example which focuses on selective information.

6.1.1 'Parallel modelling' in primate kin-structure

This section will examine Bernard Chapais' (2008) hypothesis about the evolution of hominid kin-structures to illustrate parallel modelling. I will demonstrate some features of models. We shall see the use of an underlying, developmental homology to ground the hypothesis; the construction of a 'design space' which incorporates both the conditions for

and not for the evolution of the trait; the use of homologues to construct the adaptive model; the apparent limitations of the approach. Chapais' theory also fits an evolutionary narrative, so it shows how a parallel model fits into my explanatory structure. First, the explanatory target: kin-structures in the hominid lineage.

The kin structure of *Homo-sapiens* is an outlier trait. Although primates show great variability in kin structure between lineages, particular species themselves tend to be fairly invariable. The *Pan* clade (Chimpanzees and Bonobos), for instance, is largely promiscuous and patrilocal, whereas Gorillas pair-bond (in harems) and are largely matrilocal. In contrast, human social systems run the gamut from promiscuity to monogamy, from strict patri- or matri-locality to liberal 'multilocality'. This spread is itself part of the outlier trait which requires explanation (Rodseth & Shannon 2006). At some stage in our past, we were largely invariable in kin-structure, now we are hugely variable. What has changed? How can we identify the difference-maker?

There are no analogues to human social systems available in primates. The identification of extended kin-systems (to say nothing of national or cultural identification) is unique. However, the variability does, in a sense, have an analogue. Although no other single species of primate is multilocal (in a sense both patrilocal and matrilocal), the primates when taken as a group include the whole spread.

Although this in itself is not an analogue, it does suggest labiality in the trait. If we can identify the factors which determine kin-structure across primates generally, this could allow us to identify contrasts between *Homo* and the rest of the clade. It may be we are unique in occupying a unique location in kin-structure design space – but *not* unique due to being outside of that space.

The phenomena we are interested in here is human kin-structure as measured by two dimensions. *Dispersal Patterns* describe how different lineages mix between different groups. Most primates are matrilocal – the

males tend to leave their original group. *Pan* is noticeable due to its patrilocality. *Breeding Patterns* describe connections between mating partners. *Pan* are promiscuous, Gorilla have stable breeding bonds in harems and Gibbons have stable pair-bonds. As I have said, *Homo-sapiens* is noteworthy due to exhibiting, in different cultures, almost every point along these continua.

Bernard Chapais (2008) constructed a kind of ‘primate kin-structure design-space’ and used this to generate a hypothesis about how our own lineage evolved its variability. The design-space is used by Chapais as an adaptive model. It can be used to determine which external factors determine kin-structure in primates.

His project is in three parts. He uses comparative studies of primates to construct a ‘design space’; lessons from this are then extrapolated to explain the evolutionary narrative; the final state is set based on anthropological work.

There is legitimate concern about whether he has properly set the initial conditions or defined the outlier trait correctly. He argues that the most recent common ancestor of ourselves and *Pan* had the same kin-structure as Chimpanzees and Bonobos. This is largely on cladistic grounds, and given the impoverished data set available, as well as the apparent lability of the trait, it is a very shaky position (especially considering possible falsifying evidence: the apparent dimorphism in Australopithecine). He bases his definition of human kin-structures on Levi Strauss’ concept of ‘reciprocal exogamy’, a view which is certainly not without criticisms from anthropology (Wilson Forthcoming). I am not primarily interested in these issues with his account; however, I am interested in how he goes about constructing the adaptive model. I am simplifying his story, focusing on just a few aspects of his theory.

Although Chapais’ explanatory target is a group-level phenomena, he ties his model to an organismic trait. The group-level phenomena (human kin structures) are a result of a developmental trait which has homologues in

other primates. By examining other primates, therefore, Chapais can construct a 'design-space' which matches the individual-level developmental cause to a (in this case) group-level selective cause.

The developmental trait Chapais relies on is the 'Westermarck Effect'. The *Westermarck Effect* is a theory about how kin are recognised in primate groups. There is a developmental window in the development of young whereby those in close proximity are 'recognised' as kin. This does not require any literal *concept* of kin-relationships. It is just that those who you spent a lot of time with as a child are treated 'as if' they are family. They are treated more cooperatively and are avoided in mating situations. It is important for Chapais' account that individuals are also able to recognise '2nd-order' family based on who their recognised kin recognise as kin. So if I recognise my mother, and she treats her brother (my maternal uncle) as kin, I will also recognise him in an attenuated sense.

The Westermarck effect provides a mechanism which explains primate kin-structures. If the Westermarck effect holds, then kin recognition is only viable if the relatives are in close proximity from an early age. So a parent is only recognisable if they are involved in upbringing, and a sibling is only recognisable if they are close enough in birth-order to be nearby at the right times. First I will examine the relationship between breeding patterns and the Westermarck effect.

There is a striking difference between which relatives can be recognised between a promiscuous group and a group with stable-bonds. If there are stable-bonds, particularly in a pair-bonding situation, the individual will spend formative time (be able to recognise) both their mother and father. By extension, then, they would be able to recognise the extended family of both sides. A promiscuous group is comparatively impoverished. The individual can only recognise their immediate caregiver (typically the mother), their siblings, and the extended family of that caregiver. Assuming that cooperation is based on these kin-groupings, then the opportunities for cooperation in a promiscuous group is severely limited as compared to a

stable group. Now we can turn to dispersal patterns.

Again, different dispersal patterns cause different kin-recognition. Whichever sex has dispersed find themselves in a community where they recognise no kin. In a patrilocal society, for instance, mother-daughter dyads are cut short when the daughter disperses. Only their offspring (who do not themselves disperse) are recognised. The sex which remains can recognise its kin, but half of its offspring will disperse.

We can now present what kin can be recognised in various groups though the Westermarck Effect against breeding and dispersal patterns. The table shows post-dispersal relationships.

Figure xix: Recognisable Kin Based upon Breeding & Dispersal Strategy

| | | Patrilocal | Matrilocal |
|---------------------|---------|---|--|
| Promiscuous | males | Maternal line, male siblings | No one |
| | females | Male offspring | Female offspring, Maternal line |
| Stable Bonds | males | Maternal & Paternal line, male offspring, male siblings | Female offspring, female siblings |
| | females | Male offspring | Maternal & Paternal line, female offspring |

If there is a relationship between kin recognition and cooperation, then we can envision this table as a kind of ‘design-space’. Under certain conditions selection for cooperation will lead towards stable bonds, or alternatively a shift to stable breeding could open up cooperative opportunities. For Chapais, Promiscuous males will not shift into a stable bonding strategy unless there is some kind of dampener on male-male conflict. This could be a decrease in available food (meaning that there is pressure to spend less energy on conflicts) or some new variable which

stabilizes male-male conflict (tool-use, for example).

Notice that no arrangement in the chart are the same as our lineage, who recognise everybody.

Hominids also have extra-group bonds. In other primate societies, there is no lasting bonding between groups. Human social arrangements include many such links. Chapais believes that this difference can be explained through *reciprocal exogamy*: the exchange of individuals between groups. If the groups overlap and bonds are maintained between those individuals who have left and those who have remained, then they can act as ‘bridges’ for cooperation between the groups. Chapais believes that it is male cooperation which is essential for the selective benefit which would drive the evolutionary trajectory.

Chapais takes his initial conditions as being the same as *Pan*. They are Patrilocal and promiscuous. As mentioned above there is legitimate concern about this, but for the sake of the example I will accept it. We now have the first two pieces of an evolutionary narrative.

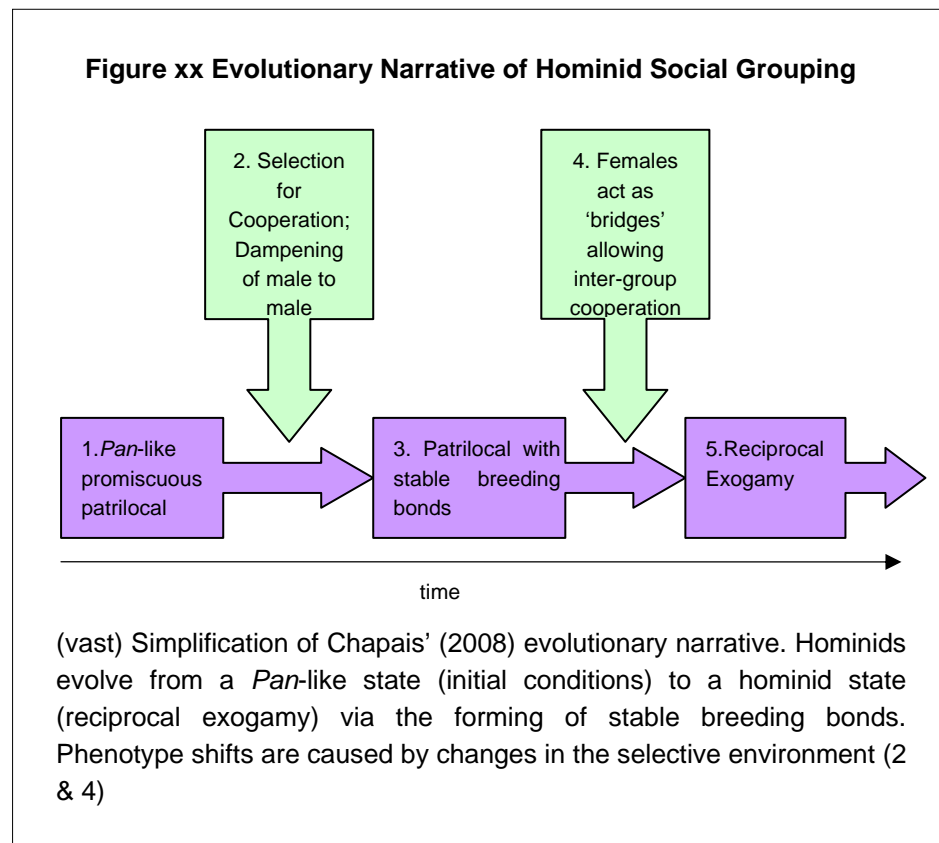
1. Setting the initial conditions: Our ancestors were Patrilocal and promiscuous with minimal relations between groups
2. Setting the final conditions: Humans have mixed philopatry and breeding strategies with many intra-group relations (according to Chapais this is due to reciprocal exogamy).

We have, then, three options for the difference maker. Chapais’ hypothesis relies on a shift to stable breeding bonds. If a group is partilocal and has stable breeding bonds, then there will be kin-recognition between dispersed females and their father. If those relationships are maintained, then bonds *between* groups can be formed.

3. Hypothesizing the Difference-Maker: The shift to stable breeding bonds opened up our ancestors’ cooperative avenues.
4. Setting the Adaptive Model: (see table above) selection for increased cooperation, coupled with a stabilizing effect to dampen

male-male competition, would cause a shift towards stable bonds. If a *Pan*-like group began exhibiting stable bonds, and the groups overlapped, then dispersed females could act as ‘bridges’ between them.

5. Constructing the evolutionary narrative:



This is a simplified version of Chapais' account. I have picked out the details necessary for my point. I certainly do not wish to commit to the viability of the project, but mean it as illustration of how, using the parallel solution, an evolutionary narrative can be constructed. There are a few features of this kind of explanation I want to point out.

In the last section I claimed that homologues were unhelpful for setting the adaptive model, but in this case we see the homologues are used in its construction. The two closest homologues of our lineage, *Pan*, play a central role in not only setting the initial conditions, but also the design-

space which Chapais uses. How do they avoid Jolly's Paradox?

Parallel models avoid Jolly's Paradox by incorporating both contrastive and comparative information. A typical adaptive model consists of a series of conditions for the evolution of a particular character or character-state, whereas a parallel model will give a series of conditions for the evolution of a suite of character-states. A parallel model of Maxillipedalism in *crustacea*, for instance, our model would include both the conditions for it to evolve, and for it *not* to evolve.

In a sense a parallel model is not an adaptive model, but simply a 'design-space' out of which adaptive hypotheses (evolutionary narratives) can be extracted.

Another point to notice in Chapais' account is the amount of extrapolation required in his evolutionary narrative. Human kin-structures are not just an outlier from the perspective of our homologues, but from all primates (and all of the animal kingdom, so far as I am aware). This means that the solid ground provided by the parallel model can only take Chapais so far before he needs to fall back onto speculation²⁶. I believe this will be typical of parallel models – although they certainly give us a solution to causal depth, they can be very limited. I will return to this point later.

It is important to see where the epistemic warrant for Chapais' theory lies. At least in part, the warrant is derived from the Westermarck Effect as an underlying, homologous, developmental process which is causally related to the target trait. Our belief in the design-space he constructs is due, at least in part, to the close relatedness of the group in his catchment area. If, for instance, it was constructed from animals picked randomly from throughout the animal kingdom (say, the kin structures of the octopus, lion and giraffe) we would wonder on what basis the claims were made. By constraining to the great apes (or maybe old-world Primates – Baboons

²⁶ Not to say that speculation is in itself negative, only that the epistemic warrant of such speculation is not longer provided by the parallel model.

could be a good data-point if the Westermarck mechanism is present) Chapais has principled grounds for selecting comparisons. The parallel nature of his data gives it credence.

I have kept the selective details of Chapais' account vague, largely because he does and, when they are provided they are very speculative. I now want to look at a different case-study which, in contrast with Chapais, focuses on the selective pressure rather than developmental homologue.

6.1.2 'Parallel modelling' in primate mating strategy

This section will explain how parallel analogues have informed models of primate mating strategies. We will again encounter the limitations of the approach, but also how 'boot-strapping' can occur as we test and construct the model across various analogues.

The use of both sexual dimorphism and testicular size to predict mating strategy in primates is an example of parallel modelling (Workman & Reader 2004). The explanatory target in this case is not the current state of human mating affairs, but the state of affairs we evolved in. We are hunting for the initial conditions of hominid mating strategy²⁷, which then evolved into the variable phenomenon we see today. I think the strategy is right in principle under favourable conditions can be executed in practice.

Sexual dimorphism appears to correlate with competition for females in primates. Dimorphic organisms tend to live in harems. Gorillas are the prime example, the males being almost twice the size of females. Silverbacks who have monopolized breeding opportunities in a harem must fight off other males, so there is selection pressure for larger size. Those with very little dimorphism tend to pair-bond or be promiscuous. Male and female Gibbons are almost indistinguishable in terms of size and they pair-bond.

²⁷ Which is not to say that the target of much of the work undertaken in this area is not aimed at discovering facts about us *now*.

Examination of dimorphism allows retrodictions to be made about hominid mating strategies in the past. Today human males are roughly twenty percent larger than females. This is closest to *Pan* (although humans show more dimorphism) and suggests a promiscuous or pair-bonding scenario existed in our past (Chapais uses this as evidence towards his conclusion that our ancestors were *Pan*-like).

Testicular size is taken as a measure of sperm competition (Harcourt 1995). The thought runs that in a promiscuous environment where females mate with more than one male, there will be a selective advantage in having more sperm. The more ejaculate, the higher the probability of breeding success. In an environment where females tend to mate with a single partner, then there is no need to spend extra resources on sperm. If this is right, then we can predict the promiscuity of a species based on its testicular size. A *polyandrous* (promiscuous) lineage should have greater relative testicular size than *monandrous* (bonding) relatives.

In baboons, for example, the relationship between testicular size and mating strategy has been demonstrated (Jolly & Phillips-Conroy 2006). Baboons which live in harems ('one male units'), such as the Hamadryas and Yellow, have significantly smaller testes than those that live in multimale groups such as the Olive and Guinea Baboons.

Using testicular size and dimorphism, then, we can predict the mating strategies of primates. A primate with larger testes will be promiscuous; one with small testes will bond. A dimorphic species will bond in harems, a less dimorphic species will either pair-bond or be promiscuous. These can be plotted in a design-space similar to the one I employed in the last section.

Figure xxi Primate Breeding Strategy Identified by Dimorphism and teste size

| | Larger Testes | Smaller Testes |
|-----------------------|-----------------------------------|-----------------------------|
| More Dimorphic | ? | Bonding, Harem (Gorilla) |
| Less Dimorphic | Promiscuous (chimps & bonobos) | Pair-bonding (Gibbons) |

This design space can be used to compare competing hypotheses. In the last section Chapais’ theory of the evolution of kin-selection in the hominid lineage relied upon our ancestors being pan-like. They occupied the bottom left quadrant. Another theory (see Chapais 2008 pp 152-156) claims that our ancestors were similar to Gorilla, occupying the upper right quadrant. One piece of evidence we could consider when comparing these theories is the dimorphism of our ancestors. There is some reason to believe (although Chapais for one disputes it) that Australopithecine was dimorphic – males were significantly larger than females. Assuming our testes size is roughly the same as it is now (thus avoiding drifting into the troublesome upper-right quadrant) then this is evidence that the Gorilla hypothesis is more likely²⁸.

So, by examining the primate clade to create a parallel model we are able to set a quantified inferential structure which can be applied across that clade. Again, part of the epistemic warrant of the approach lies in the relatedness of the lineages examined. There is an implicit assumption that homologous developmental processes are producing the phenomena that is

²⁸ To be fair, Chapais wrangles a good series of arguments to dispute the Gorilla Hypothesis (for one thing, this arrangement is less parsimonious in cladistic terms), and dimorphism in Australopithecine is not firmly established. Again, this is just meant as an example of the application of the model – not a firm argument either way.

quantified.

A worry we might have is whether this is truly an analogous inference, or just the corroboration of an adaptive model. In the first instance, we take a selective-environment/phenotype pair and project it onto a target lineage. In the second, we test our adaptive model by examining possible analogous instantiations of it. I think either construal applies to what I have to say about analogies. In a standard analogous inference, the relationship is projected directly onto the target. In the modelling case we project from the analogue onto the general model. I think relevantly similar inferential concerns exist for both versions.

An interesting question which arises from this examination is whether any primates fit into the top-left quadrant. If they do, whatever breeding strategy they employ, it will present a problem. The model predicts that we will not find a dimorphic primate with large testes. However, on discovery of an apparently falsifying case, the model need-not be thrown out. It could be that there are some exceptional circumstances which explain away the exception. Better still, this new information could be incorporated into the model – it could be bootstrapped.

An example of how a parallel-model can be boot-strapped is in Jolly & Phillips-Conroy's (2006) work. In their study, Yellow Baboons did not have testes of the size predicted by the model. They seemed too small. In response they re-examined the dimensions they were using in the model. The predictions were based on comparisons of body-mass and testicular size. Because Yellow Baboons have long, heavy arms extra weight skewed the result. "It is evidently the relatively long (and thus proportionately heavy) limbs of yellow baboons that make them *appear* to have smaller testes, when total body mass is used as the standard (Ibid pp 267, italics in original)." By looking at trunk volume (which left out limb mass) they showed that Yellow Baboons did, in fact, meet the model.

Again we see how limited parallel models can be. Just physiologically speaking (let alone behaviourally), Humans are outliers in terms of sexual

adaptation from the perspective of the primate clade. For instance, the concealed ovulation in human females significantly changes the sexual gameplan by barring males from following their fertility cycles (Workman & Reader 2004). As with Chapais' theory, the parallel model can take us only so far, but after that point any further explanation becomes increasingly speculative. Because we are inferring from the model to the initial conditions of the evolutionary narrative, we need other streams of evidence to take us further along the story.

The last two case studies have shown the general form taken by the 'parallel solution'. The adaptive model is constructed through a survey of a clade, then further refined as more examples are added. The model covers 'design space' for the possible character states of the trait in question. The epistemic warrant for this practice is in part derived from a presumed underlying developmental homology (any analogous information is parallel). The approach certainly allows for very careful, quantified retrodictions but is limited in scope. If the general model is confirmed, we are able to apply it to unique cases so long as they fit within the design-space the model is concerned with. As we have seen, if a trait lacks any true analogues in the catchment area, then our adaptive explanation becomes more speculative as we move beyond the model's purview.

In the next chapter I will argue that the Parallel Solution is a suitable solution in the appropriate context, but it is not necessary for our catchment area to be constrained in the way it prescribes. An important part of this discussion involves getting a clearer handle on what it means to be parallel, which will occupy me for the remainder of this chapter.

6.2 What is it to be Parallel?

I have defined parallel as follows: an analogy is parallel if the same developmental information is utilized in both analogues. There is a major issue here. As we shall see, by this definition all analogies are parallel.

They are all parallel by this definition because at a fundamental level life shares a common origin. Some genetic markers have origins in the deep

past (such as Pax6, discussed below) as they are held in common across vast tracts of life. If those resources are used to produce the phenotype we are interested in, then they would count as ‘parallel’. More problematic, a fundamental homologous similarity held across all life is the organic structure of genes themselves. All life (discovered so far) uses the same paired four-base genetic structure built from the same chemical compounds. This constitutes our main evidence that life on earth has evolved from a single event (Dawkins 2004). As genes themselves are developmental information, which are utilized in phenotype expression all analogies must be parallel.

But we have already agreed in chapter 4 that analogies typically lack epistemic warrant. To claim that they are warranted simply in virtue of underlying genetic information is not sufficient. Imagine using the analogy between the mammalian and cephalopod eye (analogous instances of a lens eye) to construct an evolutionary narrative about the evolution of lens-eyes. We would object to this because of the problem of causal depth. Analogies are not projectible: even if we are correct in our modelling of cephalopod and mammal eye evolution, we do not have grounds to then infer that the same evolutionary model applies in some other case. A response to this objection could go as follows. Both squid and humans hold their genetic structure as developmental homologues, therefore they are parallel. We agreed in the last section that the use of parallelism does gain epistemic warrant. This response is unsatisfactory. Why? Just having genes is not enough to create a lens eye. All kinds of eyes in the animal kingdom are built using genes, so the genetic structure itself cannot explain the particularity of lens eyes. We must reject our current definition of parallelism, then, as it leads to this absurd conclusion.

Genes themselves do not have the correct causal relationship with phenotype to give epistemic warrant. As we need some kind of mechanism for the development of phenotype, we could say they are an *enabling condition* for the evolution of eyes, but they are neither necessary nor sufficient. A genetic set-up based on a different chemical substrate could (perhaps) still

produce the same phenomena; if it was sufficient, then *all* lineages would develop lens eyes. Genes are part of the causal story but they do not have enough influence over phenotype to form the basis of a comparative prediction.

To avoid analogies being parallel as a matter of course, then, we need to find some account of parallel which includes those cases where developmental homologues infer warrant and excludes those which do not. So the pressing question is: what does a developmental homologue need in order to give warrant to an analogy?

We have seen that the correct *causal* relationship is important, so this will guide enquiry. Stephen J Gould presented this issue in a colourful metaphor which may be helpful to introduce at this stage.

For Gould, developmental information can be more or less constraining on phenotype depending on whether it is a ‘Pharaonic Brick’ or a ‘Corinthian Column’ (Gould 2002 pp 1132 – onwards; Powell 2007). If phenotype is strongly constrained by developmental information, then that information is a *Corinthian Column*. If phenotype is weakly constrained by developmental information, then it is a *Pharaonic Brick*. I will explain each in turn.

A Column built in the Corinthian architectural style must follow very specific design specifications in order to be successful. Too much variance will cause the column to collapse. Due to these constraints, if I know a column is Corinthian, I can make fine-grained predictions about its form. I can project many of the observations I make of a few Corinthian columns onto all Corinthian Columns.

Developmental information can constrain phenotype in a similar fashion. Recall my discussion on Maxillipedalism, the evolution of eating apparatus from limbs in *crustacea*. The trait has evolved numerous times in the clade, always using the same genetic information. We are able to give a mechanistic explanation of how Maxillipedalism occurs. If I know a lineage has that group of genes, I can then predict Maxillipedalism given the right

external inputs. The holding of the particular Hox genes involved with the phenomena is constraining enough to derive warrant for analogous inferences across the clade. So, if I wish to retrodict whether (say) an extinct crustacean used its fore-limbs for locomotion or eating, and lack physical evidence, then our observations of maxillipedalism in extant *crustacea* may be projected onto our target. If we have evidence that the target lineage occupied a relevantly similar selective environment then this, given the analogies, is reasonable grounds to hypothesize maxillipedalism in that lineage.

In Exodus, Pharaoh has the Israelites make bricks which are used in the construction of many of the buildings in his city. As any particular brick could be used in the construction of many different buildings, it doesn't look like many interesting predictions could be made based on them. We can exclude some uses, of course: the bricks were probably not used for boat building or hot-air balloons, but using a brick to build doesn't constrain the process of building enough for us to tell much about the structures they might be used for.

Pax-6, or 'eyeless' is a genetic example of a 'Pharaonic Brick' (see Gould 2002 and Powell 2007 for discussion in the context of developmental constraints; Callearts et al 1997 for a review of scientific work). Versions of the gene have been identified across extensive sections of the animal kingdom and there is reason to believe that its function is preserved across these phyla. It is a homeobox gene which acts as a 'master-control' for eye development. Removal of the gene causes the failure of eye development; duplication of it causes extra eyes to develop. Crucially, it does not control eye type. Splicing a human Pax-6 gene into a fruit fly will not result in the fly developing a human eye, but rather an extra fly eye. So, can we rely on Pax-6 as a developmental homologue to give warrant to the use of analogies? If I want to retrodict the kind of eye some extinct species held, can I rely on its presumed holding of Pax-6 in its developmental apparatus to grant epistemic warrant to the utilization of analogies to support hypotheses?

Because Pax-6 is passive in regards to the *kind* of eye which develops, it does not constrain phenotype enough to grant epistemic warrant for models of eye evolution. Pax-6 cannot show regularities in phenotype expression. Both cephalopods and mammals do hold Pax-6 as a developmental homologue (Tomarev et al 1996), but its ubiquity in non-analogous eyes shows that it does not constrain the process enough. Because, for example, Pax-6 does the same job in the development of lens eyes and compound eyes it cannot shed light on why a lineage might have compound rather than lens eyes. It is an enabling condition for both, but a good explanation for neither. So, like the genetic structure itself, Pax-6 is a Pharaonic Brick – it does not grant epistemic warrant to the use of analogy because it does not hold the right causal relationship with phenotype.

A developmental constraint's being a pharoanic brick or Corinthian column is relative to the particular question we are asking. For instance, Pax-6 does not constrain phenotype enough to warrant hypothesizing regularities about the kind of eyes which evolve. But, it may constrain phenotype enough to predict that a lineage will evolve visual sensory apparatus (as opposed to some other method of garnering information about the environment).

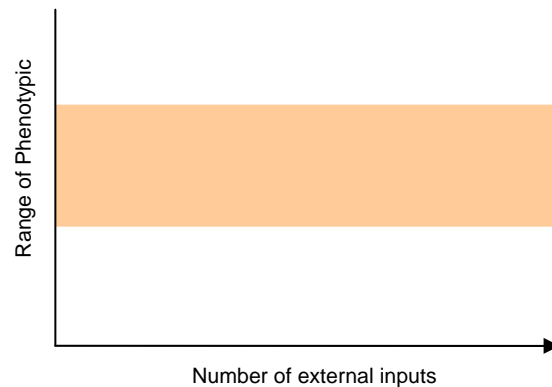
Gould, then, divides convergence into two types. When the developmental homologue has too weak an influence on phenotype to grant warrant it is a Pharoanic Brick. It is an enabling condition, but is inert in terms of the regularities we are hunting for. A Corinthian Column, on the other hand, does grant warrant. It has a strong enough influence on phenotype to count as a sufficient condition for a trait's evolution (given the right selective conditions). Presumably Gould means for these cases to be ends of a continuum – some developmental processes have more or less effect on phenotype, and thus grant more or less warrant to analogies that utilize them.

So we want our account of parallel to include Corinthian Columns, but exclude Pharaonic Bricks. For the Parallel Solution to work, the

developmental resources need to have the right level of what Woodward calls *causal specificity* (Woodward, forthcoming). Causal specificity measures the level that a particular cause affects the phenomenon of interest. In particular a more specific cause will help with counterfactual claims. For instance, if we want to understand why phenotypic expression of developmental resources varies, we are better served by examining the DNA *differences* in variants than (say) the RNA *constants*. Woodward uses a broad interventionalist account of causality. So a highly specific cause will have clear, predicted results upon intervention. A specific cause will be a difference-maker.

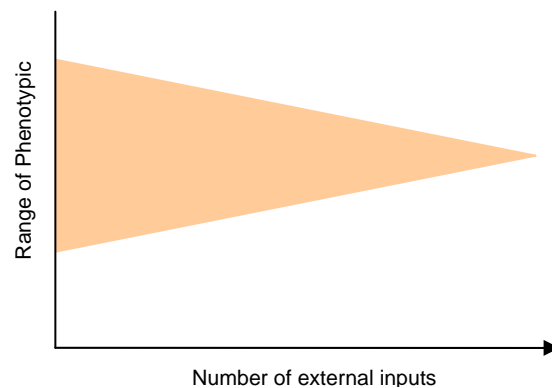
Unsurprisingly, the more a developmental system constrains phenotype, the more warrant it grants to an inference relying on parallel evolution. The more phenotypic expression is constrained, the more causal specificity is attached to the environment. In extreme cases, we could view the environmental input as a ‘switch’, determining phenotype expression. The two figures below plot phenotypic possibility against relevant environmental factors for both pharaonic bricks and Corinthian columns. In the highly constrained case, increases in environmental input will quickly constrain possible phenotype. We can confidently see the relationship between the initial conditions and the external factors. If we see this arrangement in an analogue, then, the relationship between initial conditions and environmental ‘switch’ can be confidently projected onto a target lineage. As Gould puts it, something counts as parallel “... if the underlying homology prescribes a highly distinctive, detailed and strongly determinative channel of constraint (Gould 2002 pp 1135).”

Figure xxii Pharaonic Brick



The addition of external inputs to a minimally developmentally constrained trait (Pharaonic Brick) will not decrease the range of phenotypic plasticity: the predicates are not projectible

Figure xxiii Corinthian Column



The addition of external inputs to a developmentally constrained trait (Corinthian Column) decreases the range of phenotypic plasticity. When enough external factors have been identified, we can model the environment/phenotype relationship

Now that we know what we are looking for in a definition of analogy, I will discuss the kind of answer we want. We should avoid drawing a line in the sand when defining parallel evolution, as its continuous will not be captured by a strict boundary. There seem to be two approaches for defining parallel in the literature. Traditionally an analogy is defined as

parallel if the analogues are closely related. Another approach is to claim that we must identify the developmental homologue in order to claim parallelism. I will argue that we needn't choose between these definitions.

The traditional method of defining parallelisms is by examining paraphyletic groups (Griffiths 1994). If we restrict examination to members of a particular clade (where that clade is 'small'), then the probability of any cases of homoplasy being due to common developmental resources increases. We assume a developmental homologue causes the similarity.

A stricter method would be to demand that the developmental homologues are actually identified (Gould 2002, Powell 2007). Here a research programme in developmental genetics, identifying the actual mechanism involved with development, would be required before we can claim parallelism.

I will for now take these methods as strict definitions. Can either of these accounts adequately draw a boundary between what counts as parallel, and what does not?

First, I will consider the traditional account. The question is whether there is some rule which can, in a principled manner, distinguish between a Pharaonic Brick and a Corinthian Column in terms of the size of the paraphyletic group and the number of required events within that group. If parallelisms are clumped within clades, then to differentiate parallelisms from convergence, we need to discover 1) the number of events necessary and 2) the size of the required catchment area. As Diogo (2005) asks - "How many homoplastic events of a certain character should we have... in order to hypothesise that the homoplastic development of this character was due to parallelism and not to convergence? (Ibid pp 714)" If we cannot find a way of drawing the boundaries between parallel and convergence, then the definition fails.

Imagine we using analogues to model the emergence of a trait. We dutifully restrict our catchment area to within a clade. However, what if there are striking analogues of just outside of the catchment area? Should

we then increase it? Any two lineages can be seen as part of a clade – we just need to trace their relationship back far enough. Because different developmental resources will restrict phenotype expression to different levels, one rule based on clade-size or event numbers cannot capture these differences. Without a principled way of judging when our catchment area is the right size, the traditional approach is unsatisfactory as a definition of parallel.

Russell Powell (2007) argues that we should restrict our definition of parallel to those cases where the underlying developmental information is a *direct cause* of the trait in question. The developmental cause must be *proximate*, which is to say that it cannot be masked by any other cause. Although Pax-6 is clearly a cause of eye development, other downstream developmental information determine the particular phenomena we are interested in (eye-kind phenotype), Pax-6's causal efficacy, then, is masked²⁹.

Powell's approach avoids the criticisms of the traditional account by tying parallelism to developmental information rather than paraphyletic groups. We do not need a rule about the number of events or the temporal size of a clade we are examining if our definition relies on developmental information. But we do not require such a strong prescription.

Recall my case studies of parallel modelling. It is besides the point to criticize these on the basis of not identifying the developmental mechanisms in question. The actual mechanisms involved in the Westermarck Effect and the development of dimorphism or testicular size do not need to be understood in order to justify inferences based upon them. We have reasonable grounds for assuming there is some uniting

²⁹ I have intentionally avoided the technical definitions here, as I don't think they are necessary for the account. Powell utilises Brandon's technique for determining proximate causes: cause P screens ancient cause D for homoplastic trait T if the probability of T given P & D is the same as T given P but different from P given T.

developmental process which underlies these closely related lineages because of the success of the model across the clade. Therefore, it is unreasonable to expect us to put a halt on any inferences based upon them until a reductive, mechanistic explanation of the developmental homologues themselves is provided. And so giving a definition of parallel tied to the identification of the developmental homologues is unsatisfactory.

Based on these considerations we should conclude that parallelism and convergence are continuous. Parallel analogies are such because they have enough developmental constrain to control for developmental noise. What is going to count as ‘enough’ depends upon the nature of both our question, the causal strength of the external influences and the developmental resources themselves. Being parallel is a matter of *degree*. Because of this, I think the right approach is to avoid giving any kind of definition, and instead I will briefly point to several methods of *diagnosing* parallel evolution

Both approaches should be seen as diagnostic of parallelism. If there is a reasonably closely related paraphyletic group with enough independently evolved examples of the trait, this seems fine. If the developmental mechanism is actually identified, so much the better.

In the Pax-6 case, one reason to resist it being parallel in the evolution of lens-eyes (at least when discussing the evolution of a kind of eye, rather than eye evolution versus, say, ear evolution) is because the paraphyletic distance between us and cephalopods is too great. Additionally, the developmental mechanism itself simply does not have the causal force to ground the inference. It is a Pharaonic Brick.

The Westermarck effect in primates, by contrast, should be thought of as parallel. The paraphyletic group in which it is present (which, for our purposes, is simply the primate clade) is reasonably constrained. The developmental resources themselves control phenotype expression enough to ground prjoections. It is a Corinthian Column.

So an analogy is parallel when there are reasonable grounds for believing that the trait in question is caused by a developmental resource which is homologous in the analogues and constraining enough of the phenotype. Reasonable grounds can be either close relations and a well corroborated approach (as in testicular size and sexual dimorphism) or actual identification of the developmental process (as in Maxillipedalism).

Before moving on, I want to make clear when parallel modelling is an appropriate approach. These are not intended to be hard and fast rules, but rather a guide. They are variables which would determine the level of epistemic warrant we might give to a hypothesis reliant upon a parallel model.

1. There is a suitable number of lineages available (the clade in question is not too impoverished)
2. There is a suitable number of comparative and contrastive exemplars available to construct the model
3. There is a plausible case to be made that the analogies are parallel (the trait clusters within closely related groups, the developmental homologue has been identified, or there is good reason to believe there is a developmental homologue)
4. There is a plausible case to be made that developmental resources (as opposed to selective forces) carry the bulk of the causal burden for phenotype explanation

4 is entailed by 3 as I have defined a case of parallel evolution as when developmental information does most of the constraining (is a 'Corinthian Column' in Gould's terms). If 3 is the case, then 4 will also be the case. I felt it necessary to split them in order to emphasize the rationale behind parallel modelling. Epistemic Warrant is granted on the basis of underlying developmental homologies, *not* the analogues alone.

With this account in hand, I can now move to the next chapter. Here I will argue that although parallel solution is legitimate, it is not the only use

of analogies for the kinds of questions I am interested in. I will then describe these uses.

7. A Vindication of Non-parallel Modelling

This chapter argues that non-parallel modelling has a role to play in the retrodiction of outlier lineages.

Parallel modelling is not the only solution to the problem of causal depth. To show that a solution to a problem is not necessary, all that is required is to show a different, valid solution. So my argument uses exemplars of non-parallel analogues and shows how they avoid the problem of causal depth.

In the first half I will give an abstract argument for the validity of non-parallel modelling, which will be fleshed out in more detailed case studies in the second half. I will conclude with a set of conditions for when non-parallel modelling is appropriate.

7.1 The Parallel Solution Is Not Necessary

In the last chapter I gave an account of parallelisms and I will use this to sketch two situations where analogies have epistemic warrant for fine-grained explanation, but are not parallel³⁰. The first is when selection is a strong enough force to give a basis for inferences. This can be show by examining a group of analogues. The second will be the use of other historical sciences to provide the grain. If non-parallel modelling is sometimes a valid use of analogies, then parallel modelling is not the only option, and therefore not necessary. Whether or not there are many viable or even plausible applications of non-parallel modelling will be discussed

³⁰ I should point out that in the literature those who put forward parallel modelling do not typically claim it is the *only* route, but it is at least implied in some pieces and other options are not usually explored.

later in the chapter.

Consider two situations, *A* and *B*, in which we find similarities between lineages. In situation *A*, there is a striking (analogous) resemblance relation between a group of lineages and there is reason to believe these resemblances are parallel (for example Maxillipedalism). In situation *B*, there is again a striking (analogous) resemblance relation between a group of lineages, but here there is no reason to see them as parallel. What kind of explanation do we want to give for these resemblance relations?

In the first chapter I sketched a general account of similarity. I suggested there were three possible explanations for resemblance relations. One was continuity of history, which in a biological context relates to homology. One was continuity of process, which would relate to analogy. The last was accident, which could relate to homoplastic resemblance relations which are due to different selective pressures. I claimed that an explanation could consist of any combination of these factors. What explanation would we consider most likely in situations *A* and *B*?

In *A* continuity of history plays an important part in the explanation, as they are parallel. The closer the relations and the more corroborated the hypothesis, the more we would expect this to be the case. The identification of the developmental resources themselves would further confirm our claim. I will not go into further detail about *A*, as this situation has already been explored through my case studies in the last chapter.

In situation *B*, continuity of process forms the larger part of the explanation. There may be underlying developmental resources utilized, but the distance between the lineages examined would undermine a diagnosis of parallelism. Accident may also play an important role, and how much credence we give it is based on several factors. The more striking the similarity, the more independent evolution events we have and, recalling the discussion in chapter 1 about complexity and functional ambiguity, the more complex the trait, the less likely that the similarity is due to accident.

So, if situation *B* is the case, and the trait is complex enough, and the

similarity is striking and well corroborated, then we would declare the explanation of the similarity to be due to similar selective pressures. If we were to then construct a hypothesis based on this, would it be justified?

As I have previously argued, the problem of causal depth is an empirical problem about the nature of analogous similarities, not a conceptual claim. It is not the case that analogous similarities must be shallow by their very nature, but because Natural Selection doesn't connect form to function we should expect analogous similarities to be shallow and be suspicious of inferences made based on them. But this suspicion can be allayed.

I want to give a quick example of what I believe is a legitimate case of Situation B in order to flesh out how our scepticism might be dampened. There is a surprising, striking similarity between us and (of all things) Koalas which Henneberg et al have examined (1997). Both lineages have fingerprints. What is more, the fingerprints are so similar that an electron microscope is unable to tell whether a sample is from an adult Koala or a human. So the similarity is striking, but what of it? It seems very unlikely that Koala and Humans have identical fingerprints because of continuity of niche. Although they are homoplasious, on what grounds should we consider them an analogy?

Henneberg et al do think of fingerprints as analogies, and their basis for thinking this is revealing. Their conclusion, that "... dermal ridge patterns [fingerprints] are heritable structures occurring on the skin of those mammalian extremities that are prehensile irrespective of the taxonomic affiliation of an animal... (Ibid pp 2)", is a claim which is general across all mammals. It is a robust-process explanation of fingerprints in *Mammalia*. Although this is in a sense developmentally constrained, the sheer size of the clade implies that being a member of *mammalia* is merely an enabling condition for fingerprints, they are not parallelisms. On this basis, we could conclude that the similarity is accidental. To counteract this, Henneberg and associates must convince us of selective force acting upon the trait.

The selective force which Henneberg et al call upon is adaptation for

grasping in arboreal environments. They cite three pieces of evidence for this. First, the closest relative of the Koala is the clade including the burrowing Hairy Nose Wombat (see Phillips & Pratt 2008 for cladistic analysis) which is neither arboreal, nor grasping, which lacks dermatoglyphes (fingerprints). Second, the Short-tailed Spotted Cuscus (*Phalanger Maculatus*) which is more distantly related (the suborder Phalangeriformes, as opposed to Vombatiformes) but is arboreal and grasps, does have dermal ridge patterns and lives in an arboreal environment³¹. Third, the adaptation is not for just living in arboreal environments, but specifically for grasping, because tree kangaroos (another relative), which are arboreal but do not grasp, do not have dermatoglyphes. This evidence corroborates the adaptive hypothesis by either showing contrastive information (the first and third) or comparative information (the second) which is compatible with the hypothesis.

This is the right kind of evidence to suggest that the homoplasy between Koalas and Humans is due to continuity of niche. If the trait is due to similar selective pressures, we should expect lineages in similar niches to exhibit the trait (such as the Cuscus does). That closely related species do not exhibit it ties the trait to an arboreal environment. Further corroboration would come from examining other arboreal mammals. The more cases of independent finger-print evolution coupled with a branch-grasping environment, and more cases of fingerprintlessness coupled with a non-branch-grasping environment, the more plausible our case. Does this get past the problem of causal depth, however? Just because we can agree that an explanation of Hominid or Koala resemblance in dermatoglyphes is due to them being analogies, how does the robust process (that mammals

³¹ It is not stated whether or not this represents an independent evolution event between Koala and Cuscus or not. If they are independent, than this would be an (presumably parallel) extra analogy. If the similarity is homologous, however, it is not so clear whether it would count as evidence. Additionally, given the bushiness of the Cuscus lineage, it is reasonable to enquire as to whether *all* cuscus have fingerprints, or just the examples cited.

grasping in trees evolve fingerprints) gain epistemic warrant? Can we project our analogies of fingerprints in hominids, koalas and cuscus onto other lineages

Epistemic warrant is granted here through bootstrapping. Both primate and marsupial dermatoglyphes act as corroborating evidence for the robust process that the model expresses. The problem of causal depth shows that we cannot assume optimization. In situations where evidence is carefully collated and confirmed across wide taxa, then there is no reason why warrant cannot be granted.

But is this explanation really satisfying? It is still in the nature of analogous similarities: it is in a sense *shallow*. Our original explanatory target was the amazing similarity between the fingerprints of *Homo-sapiens* and *Phascolarctos-cinereus*. The explanation is that they have fingerprints as adaptations for grasping due to living in an arboreal environment. This explains why Humans and Koalas have fingerprints – but fails to explain why their fingerprints should be so similar. A reasonable conclusion might be that the particular similarity here is accidental. So it may be the case that these analogues allow us to construct a projectible model which can tell us about other tree-grasping mammals. But it does not allow us to project the level of specificity apparent in the close similarity between us and Koalas. Here is a good time to bring in my second point.

The discussion of the use of homology and analogy in this work so far (and in the literature generally) has been importantly unrealistic. It has only attended to comparative information between lineages as a way of informing historical inferences, as if when we construct such hypotheses this information is looked at alone. Nothing could be (or at least should be) further from the truth.

History is, if not intractably messy, than at least extremely complex. The best historical hypotheses will draw upon as many inferential streams as possible. Comparative information, then, may form an important part of a hypothesis. We look to the hypothesis as a whole for epistemic warrant, not

its parts in isolation.

For instance, John Horner's (1983) theory that some species of dinosaur were altricial (nestbound and requiring parental care during youth) relies upon both comparative and fossil evidence. He and Robert Makela's discovery of fossilized *Maiasaura* nests in 1979 provided physical evidence that young were cared for. This evidence makes no sense unless examined against comparative information from bird nesting practices (Horner 1994). Basically, because *Maiasaura* nests look like birds nests, Horner concluded that *Maiasaura* babies had a similar upbringing to extant birds.

What does this have to do with the problem of causal depth? Just because analogous resemblances might themselves be shallow, it does not follow that an explanation which involves them is. The required depth could be acquired from, or in combination with, other streams of evidence. Horner's hypothesis can glean fairly fine-grained information about *Maiasaura* behaviour (to a reasonable degree of certainty or warrant) based on a combination of fossil data and comparative data from extant altricial species.

In the case of the Koala fingerprints, an examination of the process by which fingerprints develop may enable a finer grain of explanation. If there are similarities between how fingerprints develop between the Hominid and Koala lineages, these continuities could be part of our explanation (or, for that matter, part of the explanatory target itself!). Here the developmental similarities could themselves be either homologous or analogous; in either case they can help us construct a fine-grained explanation of fingerprint development in both lineages. The adaptive explanation will get us part of the way: explaining why they have fingerprints in the first place. The mechanistic explanation would get us the rest of the way by explaining why Koala and Hominid lineages are so similar. A satisfactory (fine enough grained) explanation of the homoplasy between us and Koalas requires *both* streams of evidence.

And so there are two reasons why parallel modelling is not the only way

to successfully use analogues. First, in situations where there is a non-parallel similarity between lineages, and that similarity has been confirmed across several independent examples (situation B), it is reasonable to conclude that Natural Selection *does* play an important role in that case. Such cases will probably be developmentally constrained in some sense, but these constraints will be broad and explanatorily vacuous (they are merely enabling conditions). Second, the finer grain required for epistemic warrant need not come from the analogies alone, but can be granted on the basis of other information streams. Analogies can be part of an *integrated explanation*.

In the next section, I will take up my sketch of situation B and clothe it in terms of my explanatory structure for outlier lineages from chapter 5 and a few case studies.

7.2 Non-Parallel Analogous Modelling

This section will show that in appropriate situations we can use non-parallel analogues to model outlier lineages. There are two approaches that I will explore. The first relies on using other streams of evidence to form our hypothesis. The second uses bootstrapping across several analogues to refine the model and gain epistemic warrant.

First I will examine the use of analogies to support the claim that *Homo-floriensis* is a phyletic dwarf due to selection for smaller size in an island environment. This will show how analogues can gain necessary causal depth when taken in combination with other information-streams.

Second I will follow the construction of a hypothesis about the evolution of teaching behaviour in the hominid lineage using Meerkats as an analogue. This discussion will demonstrate how the incorporation of several analogues into model construction can grant warrant.

The case studies will set me up for a more abstract discussion of the kinds of roles I see non-parallel analogues as taking in hypothesis construction and confirmation.

7.2.1 Case Study: Dwarfism in *Homo-floresiensis*

The first case study I will examine is the use of non-parallel analogous information to inform the hypothesis that *Homo-floresiensis* were of Erectine stock. My aim is to show the use of analogies as *part* of the evidence for a hypothesis. The problem of causal depth is avoided because the proper grain is provided in combination with other information streams.

Homo-floresiensis are a recent (and surprising) addition to the hominid lineage. Confirmed finds have been limited to the Indonesian island of Flores where they seem to have lived up until around thirteen thousand years ago. Their most striking characteristic is their diminutive size. The adults are thought to average around 1 meter tall (Brown et al 2004), which has earned them the nickname 'hobbit'.

The hobbits are enigmatic: some of their traits point to a phylogeny which undermines current orthodoxy in hominid dispersal. It is generally held that two hominid lineages spread from Africa into Asia: *Homo-erectus* and *Homo-sapiens*. However, if Floresiensis evolved from an earlier branch of the hominid tree, this would show that there was an earlier radiation into Asia. Perhaps *Homo-habilus*, or an earlier lineage. As such, there are two competing hypotheses about hobbit evolution. Roughly, one claims they are dwarf erectines (thus preserving orthodoxy), the other that they are habiline.

What evidence can count for either side? Remarkably, cladistic analysis provides two equally parsimonious trees. One sides with the habiline hypothesis: they emerged between 1.86 and 1.66 million years ago (a little before *Homo-habilus*). The other has Floresiensis evolving as part of the Erectine line (Argue et al 2009). So examining the character states themselves cannot resolve the issue.

We need to work out which of the following scenarios is more likely. Either a wholly undiscovered lineage of hominids left Africa sometime after 1.86 million years ago and spread across Asia. Or a group of Erectus evolved island dwarfism with remarkably habiline features. So, is it more

probable that there is a (until now) surprise lineage which left Africa and was successful enough to radiate to Flores – without leaving any other traces. Or is it more probable that island dwarfism in erectus lead to the suite of traits which the hobbits possessed?

An undiscovered lineage in the hominid tree would not be as remarkable as we might suppose. The fossil record for hominids is disappointingly sparse, although new finds are continually made. Considering the small probability of fossilization, and the small probability of an actual find, it is perfectly within the realms of plausibility that an undiscovered radiation exists. Having said this, the only reason we have to postulate this extra radiation is the Flores finds. There is no corroborating information whatsoever, no hint provided by fossil or archaeological finds. So, in a sense, our preferred hypothesis is erectine dwarfism as this requires less changes in surrounding theories (it is more parsimonious).

In a series of papers (the latest 2009) Jungers et al have challenged the dwarfism hypothesis by examining physiological traits of the Flores finds. Hobbits have several characteristics which are not merely small from the perspective of Erectus, but also primitive. Most notably, they seem more adapted for arboreal life (less perfectly bipedal) than Erectus and their brains are surprisingly small. Is island dwarfism enough to explain not just the diminution of size but also the apparent regression? I will focus on encephalization (brain size compared against body size) as it is here that interesting use of analogy has been made.

Based on developmental assumptions, the brains of Floresiensis are much smaller than we would expect. During ontogeny in larger mammals brain growth typically completes earlier than the rest of the body. So, if a lineage is a dwarf due to a shorter growth period, we should expect brain size to be correspondingly larger. So, all things being equal, as body size decreases we should expect encephalization to increase. Based on models

using these kinds of assumptions, as well as research on modern Pygmies³², the body weight predicted based upon Floresiensis brain size is half that estimated of the specimens found (Martin et al 2006)³³. In short, their brains are half the size they ought to be. And so it is much more likely that the Hobbits are habiline (or even Australopithecine), as their brain size disqualifies island dwarfism from the explanation.

So the claim is that Floresiensis cannot be phyletic dwarves because of the nature of the robust process of island dwarfism. As such, the strength of the objection is reliant on our confidence in the model of island dwarfism. This model takes information from existent human populations (see note 3 for disquiet about this) as well as from both domesticated and wild mammals. Its primary justification, however, is based on assumptions about mammal ontogeny, the developmental process by which island dwarfism occurs. There are two assumptions here. One is that dwarfism occurs by retarding later stages of growth. That dwarfism will affect brain size less than gross body size is reliant upon this. Second, brain size and gross body size must be coupled³⁴. If the developmental process which effects body size necessarily also affects brain size, then selection for smaller body will also select for smaller brain to the encephalic correspondence predicted by the model. If, however, the two can be

³² I am very suspicious of the worth of evidence provided by Pygmy populations. Although they certainly exhibit smaller size, presumably due to selection, they *certainly* do not constitute a separate species to the rest of the human lineage. As such, the difference between the kind of task facing us here (predicting encephalization change based on dwarfism as part of speciation) is astronomically different than that provided by intra-species examples.

³³ Martin et al (2006) believe the most likely explanation for this is that the specimens found are not a separate species, but rather modern humans with microcephaly. I am ignoring this hypothesis largely because I think it is clearly false. If we examine the suite of traits which Floresiensis exhibits, rather than simply brain-size, it defies credulity to imagine that this was caused by some kind of disease.

³⁴ Just to be clear, by 'coupled' here I do not mean that any change to body size will have an *equal* size change in brain size. I mean that any change in body size *necessarily* changes encephalization as predicted by the model.

affected independently, then we are unwarranted in assuming that a smaller body will correspond with a particular encephalitic range.

Weston & Lister (2009) challenge the model used to predict encephalization in island dwarfism by examining analogous data. They use two lineages of extinct pygmy hippopotamus and an extinct lineage of pygmy elephant against an extinct lineage of large hippopotamus, as well as extant variants. This data does not fit the model which Martin et al and Jungers et al use. The brain size reduction seen in *Floriensis* does fit with the analogous data Weston & Lister collate. This shows that at the very least it is possible that dwarfism could explain this level of reduction in brain size. “Whatever the explanation for the tiny brain of *H. floresiensis* relative to body size, the evidence presented here suggests that the phenomenon of insular dwarfism could have played a part in its evolution (Ibid pp 87).”

In this example analogies are used to counter an objection to the hypothesis they support. The original claim was that the brain size decrease in hobbits could not be put down to dwarfism as the traits they exhibit did not lie in the realm of possibility laid out by the robust-process of island dwarfism. What Weston & Lister’s work shows is that the original model of island dwarfism that backed up the objection is faulty.

The evidence challenges both assumptions required for the ‘late-ontogenetic model’ (as Weston & Lister call it). Their data shows that dwarfism does not always occur via the retardation of later ontogenetic processes. There must be processes which allow brain growth to be decreased more than body growth. And this possibility undermines the second assumption. Brain and body growth can be decoupled. Selection, then, could favour decreased body size without a corresponding increase in encephalization. For instance, if dwarfism is due to impoverished resources, then it could be adaptive to reduce expensive brain tissue *more* than gross body-size.

If the entire debate about *Floresiensis*’ origins centred on which model of island dwarfism was the most appropriate then we would have reason for

disquiet. Dwarfism in primates is rare: parallel information, therefore, is thin on the ground. If Floresiensis is a dwarf primate, then, its dwarfism is an outlier trait. Bronham & Cardillo (2007) examine island dwarfism in primates, but this largely serves to demonstrate that generalizations made across mammalian taxa about dwarfism include the primate clade. Their data shows that the developmental pre-conditions for island dwarfism are present in primates. Given the lack of parallel information, then, on what basis would we grant epistemic warrant to a hypothesis about hominids whose only basis was comparative data from Elephants and Hippopotamus? On what basis can we project from these large ungulates to a hominid?

This question considers the claim in isolation of the wider debate. We need not draw only on analogous data to support the hypothesis that Floresiensis are phyletic dwarves. This hypothesis is also supported by current orthodoxy in hominid dispersal patterns. Our confidence in current orthodoxy (and corroborating evidence for that confidence) actually counts as evidence *for* the Erectine hypothesis³⁵. We know, for instance, that late Erectus inhabited nearby regions (Java) – which gives credibility to the theory on biogeographical grounds. Additionally, further examination of the developmental mechanics behind island dwarfism or the decoupling of body and brain growth in ontogeny, could count as extra evidence. If we had a clearer idea of how selective pressure for dwarfism effects ontogeny (if the robust process of dwarfism was better understood developmentally) then this, assuming it corroborates the Erectine theory, could be bought to bear.

It is too early to tell whether or not the Erectine or Habiline theory will become accepted. This depends on further work into the selective and developmental processes at work in island dwarfism and the robustness of

³⁵ This is not to say that orthodox solutions are always correct (I do not mean to sound overly conservative here), but just that evidence for a particular theory will count as evidence for any corollary theory which that evidence is consistent with.

current orthodoxy about hominid dispersal. My point is that the use of analogues to justify the Erectine hypothesis do not gain epistemic warrant based on the analogues in isolation. They gain their warrant in the context of the wider debate. In isolation, the claim is suspect due to the problem of causal depth. But we should examine it in combination with the rest of the evidence for the hypothesis it purports to support.

In this example, analogous information has been a side-line to other streams. Fossil data (or lack thereof), for instance, has been the main driving source of hypotheses. I want to turn now to a case where analogy is the driving force behind the theory and show how epistemic warrant can be granted in this kind of situation.

7.2.2 Case Study: Teaching in Meerkats

This section examines the use of analogous data to inform hypotheses about the evolution of teaching in the hominid lineage. It will demonstrate an evolutionary narrative in a non-parallel context and show how epistemic warrant can be granted for analogous data by bootstrapping across analogues.

The teaching hypothesis discussed is meek. It takes a functional definition of ‘teaching’. An individual is teaching just in case they modify their behaviour in some way which does not benefit their carrying out of the skill in question, but increases the chance of uptake by an observer³⁶. This behaviour requires no fancy cognitive equipment; there is no need for intentionality, decoupled representations or a theory of mind. The behaviour can be completely automated. As such, hypotheses based upon it

³⁶ This is a simplification of the definition given by Caro and Hauser (quoted in Hoppitt et al 2008 pp 1) “An individual actor A [the *tutor*] can be said to teach if it modifies its behaviour only in the presence of a naive observer, B [the *pupil*], at some cost or at least without obtaining an immediate benefit for itself. A’s behaviour thereby encourages or punishes B’s behaviour, or provides B with experience, or sets an example for B. As a result, B acquires knowledge, or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do so, or would not learn at all.”

cannot provide a full explanation of teaching in humans. I am also taking it as an assumption that teaching is in fact an adaptation, which meerkats in fact possess.

Our explanatory target is a shift from what Sterelny calls *by-product engineering* (the environment is inadvertently organized to facilitate learning based on adult lifeways) and *protected trial and error learning*, to *true teaching*. Teaching adults do not merely protect their offspring, but “... actively intervene in the process [of learning]. They make certain aspects of the task salient. They ease the task by providing especially simple exemplars or by partially solving it. They give repeated opportunities to practice it (Sterelny 2003 pp 158).” None of these activities require intentional teaching but they may be part of the behavioural and cognitive toolkit which acts as an exaptation for more demanding cognitive faculties. So by ‘teaching’ here I am referring to a minimal functional definition.

Teaching is an outlier trait in Hominids. It is not present in our close relatives. The great apes, *Pan* in particular, are champion learners. Many chimp groups are dependant upon socially transmitted skills such as nut cracking or termite ‘fishing’. These skills, however, are not taught but learned via *inadvertent social learning* (a term which combines by-product engineering and protected trial and error learning). A chimp mother will not modify her behaviour when she is termite fishing and her offspring is near. The offspring will pick up the skill through trial and error guided by their interest in actions taken by the parent..

There is, then, an adaptive question begged by teaching. Assuming that our ancestors were non-teaching inadvertent social learners, in virtue of what did we evolve into teachers? I take it that the shift from inadvertent social learning to (minimal) teaching was a fairly early step in hominid evolution, as opposed to something which only emerged once full-blown intentionality and imitation (or even language) evolved. I am not sure, and will not examine here, whether we should be happy with placing the emergence of teaching this far back. For the sake of the example, I will take

it as a given.

Let us take our ancestors to be *Pan*-like in terms of learning and teaching. So our initial conditions are modelled on Chimpanzees and Bonobos. These include inadvertent social learning and a selective advantage for skill uptake. In a Chimpanzee band which gets a significant amount of nutrition through termite fishing, then there is a selective advantage to parents if offspring learn that skill. To discover the difference-making variable, we want to find contrasting information between this initial state and an adaptive model.

Recall that I outlined a particular structure for non-parallel analogue models. In such cases we expect developmental information to be an enabling condition for the emergence of the trait, so the hypothesis will include (at least tacitly) a developmental requirement. This will interact with selective requirements which in combination are sufficient conditions for the trait in question's evolution. In this case Meerkats are used as an analogue to construct the adaptive model.

Thornton & McAuliffe (2006) report observations and experiments with wild Meerkat populations which provide clear evidence of teaching. Meerkat adults frequently hunt and kill scorpions, which considering their non-immunity to scorpion venom is not a simple prospect. Meerkat pups have to learn how to hunt scorpions, and this is facilitated by adults in their troop. In response to begging calls from pups adults will provide partially disabled scorpions. This happens in three stages. Youngest pups are provided dead scorpions. Intermediates are given live scorpions with disabled stings. Finally a live, fully functioning scorpion is provided. This is a case of teaching: there is no direct benefit for the adult in this behaviour, and it improves the chances of the pup learning the skill³⁷.

³⁷ Thornton & McAuliffe's experimental work focused on the behaviour of the adults given particular cries from pups. They do not show that this behaviour actually improves uptake of the skill. However, it is very plausible that it does.

Hoppitt et al (2008) use Thornton & McAuliffe's data to construct an adaptive model of teaching behaviour evolution. The enabling developmental variable they point to is inadvertent social learning. In order for teaching to be effective, young must have the cognitive nuance to learn through trial and error. They also provide two selective variables. First, there must be a selective advantage for the tutor if the pupil picking up the skill. If skill uptake does not in some way increase the fitness of the tutor, then the behaviour will not be visible to selection. Second, inadvertent social learning must be inadequate (or at least less efficient) for passing on the skill. There must be selection pressure for a skill which mere trial and error learning does not easily pass on.

The model fits Meerkats well. Meerkats (like most mammals) do exhibit inadvertent social learning, particularly during pre-adulthood, so they have the developmental precondition. As we may suppose, a scorpion-hunting meerkat is generally fitter than a non-scorpion hunting meerkat³⁸, and as they are obligate cooperative breeders, it is reasonable to claim that it is in the interest of any conspecific for a pup to pick up the behaviour, whatever the specific familial relationship between them. A plausible case could be made that group-level selection plays an important role here. But also, given cooperative breeding, it is in the interests of all adults if the young become self-sufficient earlier as they can then concentrate on foraging for themselves – so a group-level story is not necessary. At any rate, the first selective requirement is met. Scorpion hunting is not a skill which lends itself to trial-and-error learning. So the second selective requirement is reasonable.

Teaching behaviour in *Homo-sapiens* (the final condition) also meet the model. Humans can learn by trial and error. It is (presumably) in the

³⁸ The statistics on scorpions as a food source seem less than promising. Thornton & McAuliffe report that 4.5% of meerkat prey biomass is made up of the scorpions they studied. Having said this, I have no idea of what constitutes a significant or insignificant amount.

interests of parents for their offspring to learn the various skills and behaviours necessary for navigating our social world. The skills we learn are complex and not easily picked up through trial and error.

So, recalling my framework for adaptive explanation of outlier traits, we now want to compare and contrast our initial state with the adaptive model. As we can see in the table below, chimps and bonobos both exhibit inadvertent social learning (in spades) and it is reasonable to suppose that there is a selective advantage to the tutor. However, the kinds of skills passed on in chimp groups are well suited to trial and error learning.

Figure xxiv Initial State vs Adaptive Model

| | Initial State (<i>Pan</i>-like) | Adaptive Model |
|---|--|-----------------------|
| Inadvertent Social Learning? | Yes | Yes |
| Selection Advantage for Tutor? | Yes | Yes |
| Skills unsuited for inadvertent social learning? | No | Yes |

The discrepancy between the adaptive model and initial conditions, then, is in the kind of skills passed on. *Pan* skills such as termite fishing and nut cracking are well suited for trial and error learning. They are repetitive, safe, and typically carried out in an environment where young can interact with adults. Scorpion hunting by contrast is fast, dangerous, and typically done away from home. So the difference making property Hoppitt et al propose is a shift in the kind of skills required for success in the hominid lineage. “Unlike other apes, in humans, teaching could have been favoured by the requirement to transmit complicated skills and technology that are not easily acquired through inadvertent social learning (Hoppitt et al 2008).”

Perhaps a shift towards obligate hunting, or some kind of tool use, could have provided the impetus?

There is an issue with the hypothesis as stated in terms of causal direction. Is it the case that the evolution of teaching opened up avenues which allowed for the evolution of hunting or tool use? Or is it that the evolution of these complex skills led to the evolution of teaching? My hunch is that each would scaffold the other. If passing on these skills requires a modicum of teaching, and teaching requires the impetus of these skills to get going, then it seems reasonable to suppose that a slight shift towards proto-hunting, or proto-complex tool use (or whatever), could drive teaching behaviour which in turn would allow better skills, and so on.

Now that we know the bare bones of the hypothesis, there are two questions. How do we test it? How then do we fill in the details? I will take each in turn. As stated the hypothesis is possible, but is it plausible? Its only evidential basis is a single mammal. And not a closely related one at that: Meerkats are *Carnivora*, sharing an ancestor with our lineage around 85 million years ago (Dawkins 2004). What basis could we have for thinking that an observation of a distantly related animal with a dramatically different lifestyle could be projected onto our lineage?

My previous solution is less applicable in this case. If other streams of information to provide the required grain, those streams must exist and be transparent enough to grant warrant. Behavioural information is notoriously difficult to discover from the indirect evidence provided by paleoanthropology or archaeology (Andrews 2009). However, see Tehrani & Riede 2008 for a discussion of the relationship between material culture and teaching. I think it fair to claim the hypothesis is, in a sense, an integrated explanation. It incorporates other streams of information to set up the initial conditions, and it may be that specificity of information here could carry over to the adaptive model. However, in this case I am concerned with increasing the epistemic warrant of the adaptive teaching model *itself*.

The hypothesis can be corroborated through application to other analogues. If there are numerous, disparate and independent evolution events of teaching, then it is reasonable to infer that Natural Selection plays an important role in its evolution. Developmental information will be a 'Pharoanic Brick'. The more examples of teaching analogues we discover, the more likely it is that continuity of niche is the right explanation for the similarity. The more these analogues fit our model, the likely that it picks out a robust process. If we are certain of the robust process, then it grants warrant to any actual-sequence explanation which relies upon it.

So what other cases of teaching in animals are there? Before Caro & Hauser (1992) suggested their functional criteria, it was generally believed that teaching was a unique hominid trait. Once the application was applied numerous possibilities were identified. Hoppitt et al cite possible teaching in eusocial insects (ants and bees), non-human primates (Callitrichid Monkeys), *Carnivora* (Cheetah, Meerkats, domestic cats) and birds (Pied Babblers and domestic fowl). Teaching has also been proposed in *cetacea* (Marino et al 2007). Even allowing for common descent in each group (which is unlikely in some cases), if these were empirically confirmed we would have five analogues available³⁹.

Work which is not being carried out is testing for falsifying cases. Most importantly, are there lineages which meet the three criteria and yet do not teach? Given the strong relationship between teaching and highly complex skills in the model, if we find negative data of this type it would certainly be

³⁹ I am uneasy about the inclusion of insects into these lists of corroborating analogues. The main issue I think is scepticism about the developmental criteria being met. I would not be surprised if some species of ants and bees do engage in inadvertent social learning in some form, so perhaps something can be learned from them. There are other cases that I do not think much inferential weight can be granted. Simon Conway-Morris (2003)'s assertion that the symbiotic relationship between leafcutter ants and a fungus is an analogue of agriculture in *Homo-sapiens* is, I think, unfounded. This is because he cannot point to a common developmental requirement which could act as an enabling condition.

an issue.

Having said this, the number of possible teaching analogues suggests that we do have a legitimate case of Natural Selection being strong enough to warrant cross-taxa modelling. I think a research programme which aims to confirm teaching behaviour in these lineages, and then uses this to inform and corroborate the analogue model, is promising.

Clarke (forthcoming), for instance, examines how feeding calls in White-tailed ptarmigan (a species of alpine grouse) influences diet-choice in their chicks. “White-tailed ptarmigan hens display a multimodal signal composed of food calling (a distinctive guttural clucking) and tid-bitting (dropping bits of a food item with active head bobbing) only in the presence of their precocial chicks... Invariably, the chick then pecks at and consumes morsels of the specific food item indicated by the hen (Ibid pp2).” Clarke makes a fairly good case for teaching. The hen points out food items which are protein rich (and thus important for survival) and difficult to identify. In an alpine environment food is scarce so a reliance on trial and error learning could lead to starvation. It appears that chicks retain eating preferences into adulthood, and so on. Clarke resists fully committing to a teaching hypothesis but points towards new research which could confirm it. This study and others like it can serve to increase our certainty that Natural Selection does in fact shape lineages towards teaching given the kind of scenario Hoppitt et al discuss.

So I have answered the first question: the hypothesis may be tested by examining its predictions across other analogues. If it is corroborated by several (and not clearly falsified by too many) then we should be confident of it. Answering this question, however, does not appear to counter the problem of causal depth. Both our model and hypothesis it has generated is still vague. The theory is coarse-grained: the ‘mechanism’ is the relationship between any particular skill and inadvertent social learning. A finer-grained model might tell us whether, say, hunting or tool-use are more likely candidates in the hominid case. No matter how confident we are that

teaching will evolve given inadvertent social learning, a selective advantage for the tutor and skills which are hard to learn, how are we to work out which skill drove the adaptation in the hominid lineage? Both hunting and tool use fit the model. Like the two hypotheses about dinosaur extinction in the second chapter, the process lacks the causal depth to let us choose between them. So the more difficult question, then, relates to the details of the hypothesis: how do we fill them in?

It may be the case that we cannot. Not all historical information is recoverable. The vague answer given for teaching may be the best we can do in some situations. Having said this, it is a better answer than could have been provided without reference to analogues. There may be some things which could extend the inference, however.

I have (largely for the sake of the example) ignored the use of indirect evidence from paleontology and the like, but there is another stream of information which could help refine our model. Maybe some analogous information is more pertinent to our explanatory target than others. For instance, Meerkats and Grouse teach very different kinds of information. Meerkats teach a particular skill whereas Grouse make particular aspects of the environment more salient. It may be that different variables are more or less important given these differences. There could be differences between how these different kinds of teaching evolve. These differences could be more or less applicable to the hominid lineage. This kind of information will refine the model.

So the problem of causal depth can be (at least partially) combated by corroborating the model across analogues. Extra detail could be gained through bootstrapping by examining the particulars of the lineages in question. The groundwork for a more ambitious solution will be given tentatively in the coda.

7.3 The Role of Non-Parallel Analogy

I will now draw out some general points about the role of non-parallel analogies.

In his criticism of Simon Conway-Morris' use of convergent evolution to support the claim that there are massive constraints on evolutionary paths due to Natural Selection, Kim Sterelny (2005) suggested that we think of regularities in evolution as 'conditional inevitabilities'. This is to say that although we cannot make claims about life in general, we might be able to discover regularities in how evolution unfolds given certain historical conditions or constraints.

In my discussion of parallel modelling, I effectively claimed that parallelisms can give us grounds for postulating conditional inevitabilities. In *A* situations (when there are striking similarities across parallel analogues) we conclude that developmental information constrains the process enough to postulate inevitability *if* that developmental constraint is present and *if* the correct selective pressure is present. My case for the use of non-parallel analogues is quite similar.

Situation B consisted of a striking similarity between two non-parallel analogues. The tempting conclusion is that the resemblance relation is due primarily to Natural Selection. Selection has enough causal force that its signal is not obscured by noise from phylogenetic history in this case. Again, *if* the developmental information is present as an enabling condition and *if* the correct selective pressures are present, then the trait will evolve. Here we must be cautious of the potential role of accident in explanation: drift and other non-selective factors could play an important role in shaping the resemblances.

The issue is here is twofold. First, how do we tell that situation B is in fact the case? How are we to tell that a striking resemblance between two lineages is due to those lineages occupying the same niche, rather than the similarity being accidental? There is a danger of 'cherry-picking' our examples to fit our hypothesis. How, then, do we establish that these similarities are of real significance. In Griffiths' terms, how do we take a group of striking examples and construct a "... robust ecological theory (Griffiths 1996)"?

Second, even if we have established that non-parallel analogues can constitute a conditional inevitability, given the problem of causal depth, what possible *use* could they have? The kinds of explanations generated by these cases seem abstract, shallow and unsatisfactory.

My response to the first issue is as follows. Imagine that situation B exists across several examples. There are striking, non-parallel similarities between a group of lineages. Take the meerkat example from the last section. We projected a selective story from meerkats onto our own lineage. Given the range of choices for projection on offer, it would be reasonable to worry that the examples are cherry-picked. How can we assure ourselves that the similarities are not merely accidental?

There are three factors, which I have already mentioned, which should undermine scepticism about cherry-picking. I don't think a particular rule is necessary (as epistemic warrant is itself a matter of degree) but our certainty of picking out a true case of situation B depends upon the number of data-points, the complexity of the trait, and the degree of similarity.

If, for instance, we were able to point to more lineages, not closely related to either meerkats or hominids, which also fit the hypothesis this would give the sceptic pause. The model/hypothesis makes predictions not just about our target lineage, but any lineage which meets the conditions specified. There is a relationship between the number of non-parallel analogues and our scepticism about cherry-picking. As the model is corroborated, it becomes more likely that we are identifying a robust process – that we have found a true B situation.

Similarly, the complexity of the trait should increase our certainty. Teaching behaviour is a striking trait and (assuming it is an adaptation) its functional purpose is relatively limited. Some examples are more obvious – both bats and birds and pterosaurs (who we have never seen fly) have analogous wings. We know this because the complexity of wings and the specificity of the requirements of occupying an airborne niche allow us to

infer their function. So, if a trait is complex (and the complexity is borne out in analogues), it is likely that Natural Selection played a central causal role in its evolution.

Finally, the level of similarity also goes towards dispelling scepticism. I have previously mentioned the principle of common cause: we should prefer a single explanation for similar phenomena. Our preference for the principle is related to how close a similarity is. Unlike homology, the similarities in analogy are both in terms of trait and environment. We might give credence to the theory that humans and Koalas evolved fingerprints due to a grasping arboreal environment because both the similarity in the trait and the similarity in the evolutionary niche are close. If we think the resemblance-relations weak, we would be less inclined to accept it.

I have responded to the second issue in various ways. The most effective response is to emphasize the role of analogy as a part of an explanation. When analogous models are integrated with other streams of evidence they can play an important, sometimes essential part. We saw this in the use of hippopotamus and elephant to support the erectine-dwarfism theory for hobbits. Here epistemic warrant is granted to the hypothesis as a whole. Maybe each stream when taken alone is insufficient to establish warrant, but in combination they can ground an explanation.

Recall my structure for evolutionary narratives. Here there were three sets of variables. They were the initial conditions, the final conditions and the adaptive model. In the fifth chapter, I argued that analogies can inform the adaptive model. If we have fine-grained information for the initial and final conditions provided by homology, field studies, palaeontology and so on, it may be the case that the analogies gain warrant as part of an integrated explanation.

The process of bootstrapping an analogous model across several examples can also provide depth. Variables which are central in some analogues may be less important in others. Examining a large group can help us pick out the important variables, and tell us under what conditions

those variables are sufficient. Aspects of the trait in question, or the evolutionary narrative that leads to it, might vary in important respects based on historical factors. Examining a large group could bring these out.

And so the role of analogies is in informing the adaptive model. Epistemic warrant is granted in non-parallel cases by a combination of finer grain through bootstrapping across several exemplars and in reference to the explanation that they form a part of.

I am now at a stage where I can articulate the conditions for non-parallel modelling to gain epistemic warrant.

1. There must be enough analogues to give grounds that Natural Selection does shape phenotype in the way proposed by the model (that it does enough of the causal work)
2. There must be reasonable grounds for assuming an enabling developmental condition is held across the analogues

EITHER,

3. The analogy is part of an *integrated solution*. There are other streams of data which corroborate the hypothesis, gaining the causal depth required for warrant

OR,

4. There must be enough information across the analogues to allow us to increase specificity by bootstrapping.

So if these conditions are met we have solid grounds for using non-parallel analogues to construct robust evolutionary models. The problem of causal depth is avoided through bootstrapping or independent corroboration.

Before finally concluding, I want to examine the use of non-biological analogues in modelling outlier lineages. This will be the topic of the Coda.

Coda

Whenever a science is declared ‘complete’, a common example is cited to dissuade such hubris; the attitudes of some physicists at the turn of the 20th century. In a lecture in 1894, for instance, the physicist Albert Michelson made the following claim: “... it seems probable that most of the grand underlying principles have been firmly established and that further advances are to be sought chiefly in the rigorous application of these principles to all phenomena... the future truths of Physical Science are to be looked for in the sixth place of decimals (Michelson, quoted in Horgan 1996 pp19).” Such statements were made directly before the revolutionary changes in physics which characterized the 20th century: relativity and quantum theory.

My project so far has been about the *limits* using animals in the reconstruction of evolutionary narratives, and I think this project runs similar risks to the claims of these physicists. They, and perhaps I, have underestimated two things: the ingenuity of scientific thought and the strangeness of the natural world. With this worry in mind, then, I want to try extending the meaning of analogy into non-biological domains.

The application of concepts from the biological sciences to other domains is not uncommon. ‘Universal Darwinism’ attempts to apply Natural Selection to the social sciences (particular in memetics and economics), Cosmology, History, and so on... (Dennett 1996). My approach is to suggest that some of the principles I have discussed in a biological context might also hold true in non-biological contexts and, crucially, this can help us understand biological phenomena.

In chapter seven, I argued for a principled basis to ground the use of disparate analogues to model outlier lineages. I claimed that epistemic

warrant could be granted provided enough corroborating analogues were available or if the analogue was used as part of an integrated explanation. An important constraint on this discussion was the availability of analogues. If none exist, then we are forced to repeat Kaplan's (2002) conclusion in regards to the use of the comparative method in the hominid lineage: analogues cannot shed light on our explanatory target.

Sometimes the application of *non-biological* analogies can inform a biological explanation. There can be epistemic and inferential continuity between biological analogues and both man made artefacts and 'true' models (in Weisberg's sense). If I am right that such continuity exists, then my discussion of non-parallel analogues will also apply to modelling, both physical and conceptual. If this is the case, then we needn't despair at a lack of comparative data: we may construct our own.

Not all models or artefacts are analogies. Some are merely attempted representations for the purpose of education – the models of extinct fauna from the crystal palace, for instance (Secord 2004). Other physical models can be important to scientific theorizing, as Watson & Crick's model of the double helix famously demonstrates (De Chadarevian 2004). I claim that *some* models meet the requirements to be analogies of biological systems. In this capacity they can both inform us about the functional import of adaptations, and inform robust processes which can generate adaptive hypotheses.

In virtue of what are two traits analogous? They must be similar in some striking sense. They also must be adaptations: traits that have evolved in response to some selective process. The traits must have evolved independently. And they must hold the trait due to *the same* selective process (otherwise the similarity is accidental – I will cover what it means for a designed object to 'evolve' below). In the context of my general account of similarity-explanation, their similarity must be due to continuity of process. My claim here is simple. If an artefact or a model 'evolves' a relevantly similar 'trait' to some biological one, through what approximates the same

process, then it can count as an analogy. It will pick out aspects of some robust process which could ground a retrodiction.

There is an objection I want to discuss. In the last chapter, I argued that there must be some developmental resources common to the analogues. These act as an ‘enabling condition’. This requirement ensures that we are picking out the correct phenomena in our analogies. Just because both ants and bees meet the functional definition of ‘teaching’, does not mean ants and bees inform a model of how teaching evolved in the hominid lineage. For it is unclear that eusocial insects evolved teaching via inadvertent social learning, and it is almost certain that we did.

If analogues must share a developmental condition there appears to be a problem with the idea of non-biological analogues. A physical model, or a conceptual one, does not appear to have developmental resources. They are not biological, and do not have genetic information. They cannot be genuine analogues.

This objection is, I think, easily met. The reason for pointing to the developmental requirement is to *constrain* our inference. We want to make sure that the analogues we are pointing to evolve by similar trajectories. In non-biological cases these constraints can be *approximated*. Because modellers have control over the variables of the model, they can set these in a way that mirrors their target system. So the developmental requirement can be met insofar as the modeller must approximately, and appropriately, represent the developmental constraints on the target system.

In the first chapter I argued that our justification for predicating some selective-function to a trait is independent of evolutionary theory. We do not identify something as a ‘wing’ in virtue of it being selected for flight. Rather, there are certain engineering facts which (give the right physical conditions) so constrain possible wings that we are able to confidently diagnose function from form. We recognise them as similar in terms of use-function, not selective-function. This discussion is as true of man-made artefacts as it is of biological morphology. The same set of engineering

facts enable us to recognise both the wings of an aeroplane and those of a bird.

Technology and biology frequently solve a problem in similar ways. Sometimes we take our inspiration from biology, but sometimes science and nature ‘evolve’ the same solution independently. An arresting example is the discovery of echolocation or ‘bio-sonar’. Echolocation is, broadly speaking, a method of garnering spatial information from the environment via the emitting of a wave (be it radio waves as in radar or sound waves in sonar). As the wave hits objects in space they will ‘echo’ back to the emitter. This information can be used to calculate the position, size and velocity of objects in space similarly to a visual system. Donald Griffin and Robert Galambos established the use of sonar in bats in 1938 and in 1952 Kellogg and Kohler discovered it in cetaceans. This came as something of a surprise to physicists who, during the Second World War, put considerable effort into the development of both sonar and radar. In fact, Griffin’s theory was met with considerable resistance – it seemed very unlikely that a technology only just being discovered by modern science could have been present in biology. The evidence was incontrovertible, however (see Jones 2005 for an overview of echolocation and Dawkins 1986 pp 23 – 36 for a discussion on the parallel discoveries of sonar and echolocation).

This is the same design response to the same problem in very different milieus. Both aircraft and bats share a problem: how do you navigate in a lightless environment? The solution is the same - instead of relying on photons interacting with objects, rely on sound (or radar) waves. I do not think it plausible that sonar literally evolved by Natural Selection (there is no clear replicating, heritable unit for selection to act upon). However, I think it is reasonable to say they ‘evolved’ insofar as both are functional responses to the same design problem. This is a case of analogous evolution – the traits are similar; they are both ‘adaptations’; they were arrived at independently; and arrived at in response to a relevantly similar selective process. There is an important difference to the processes here, of course. One is literally selected by a guiding intelligence - it is *artificial*

selection.

There are pertinent differences between artificial and natural selection. I will first discuss these in a biological context before moving to artefacts. Traits under artificial selection, due to the guidance provided, can have selection costs mitigated in a way not open to natural selection. In an important sense, the suite of traits exhibited by modern domesticated sheep were probably not open to their ancestors. The overproduction of wool presumably uses resources which, in a natural environment, could be better utilized in other areas. This is not to say a plump, woolly merino would be necessarily outperformed by a scraggily wild sheep⁴⁰. Or that extra wooliness was not a possible pathway based on the developmental resources available (this is obviously not the case). The claim is that a move towards increase wooliness infers no obvious advantage, and almost certainly involves some cost. Due to this, wild sheep populations (if under strong enough selective pressure to avoid drift) will not evolve woollier coats. It is only through the actions of their domesticators, who have preferentially bred for wooliness and mitigated whatever costs there are through the provision of food, care and protection, that something like a Merino can evolve.

Domesticity could also be understood as Natural Selection in an unusual selective environment. The point is that this case of ‘artificial’ selection is a middle ground between paradigm cases of Natural Selection and design.

For artefacts, literally designed objects further costs are mitigated. The process by which sonar technology ‘evolved’ is different to how bat echolocation (or wooliness in domesticated sheep) evolved. Sheep and bats are restricted by their biology. Without very advanced genetic engineering, changes must be largely gradual and haphazard. Modern engineering, by contrast, can evolve in leaps due to imagination, experiment and a

⁴⁰ The general outperformance and replacement of indigenous wild species with feral lineages is testament to the selective prowess of some domesticated animals.

theoretical understanding of the mechanisms involved. Echolocation almost certainly evolved over a much longer timescale than sonar.

So artificial selection (both biological and technological) differs from natural selection in one important respect. Artificial selection removes constraints. In the sheep case selective constraints are removed, and in the sonar case ‘developmental’ limitations are further limited. Design is constrained by technological competence and resource availability – but nothing as stringent as a biological developmental system. As such, the availability of a particular design to artificial selection does not mean that that design is open to Natural Selection. All forms which are available to natural selection are included in the set available to artificial selection, but some forms which may be artificially selected are not included in the set open to natural selection.

The lesson here, then, is that examining artificially selected objects, particularly engineering and design (as opposed to domesticity⁴¹), can tell us about the limits of physical possibility. They can inform a robust-process which both explains why a particular design works, and more importantly why a particular design is, or is not, *physically* possible. So a morphospace may tell us what the logical limits of a form is, and an ‘empirical morphospace’ (McGhee 1999) can tell us which areas of those possible

⁴¹ One way of viewing domesticity is as a fairly large-scale experiment on developmental plasticity. Some animals have been bred for functional purposes (horses have become larger and stronger, cows more placid and milk-rich and so on), but others purely for novelty. These ‘experiments’ can tell us something about the range of developmental potentiality open to different developmental systems. For instance, it has long been noted that the domesticated dog seems to have a much wider morphological potential than other domesticated animals, cats for instance. Cats have been bred for novelty as much as dogs, and yet dogs have demonstrated enormous flexibility. It is clear that a Maine Coon and a Sphynx are both cats. It would be less clear upon seeing a Great Dane and a Chihuahua that they would be the same species (see West-Eberhard 2003 pp 298-299). Why?

Also, of course, one of the main lines of evidence for Darwin’s theory of Natural Selection came from observations of artificially selected domesticated animals.

forms are actualized, but the examination of artificial analogues, and the engineering and design regularities they discover, can set physical limitations to morphospace. They can tell us why some areas are unoccupied, and suggest why some areas are.

I will put the point in terms of a traditional morphospace. Examining the mathematical properties of shells can tell us about the logical space of shell design. Actual shells can then be plotted against the morphospace. Contrasting the morphospace with the ‘empirical’ morphospace sets a question: why are some realms of possibility crowded, and others empty? If we can discover *physically* possible ‘shell-space’ this will help by disqualifying some areas of logical morphospace. Physical possibility of shell design can only be determined in reference to a set of regularities (robust-processes) about the physical properties of shells.

I will illustrate these two uses, human artefacts as making design aspects salient, and informing a robust-process, using examples from J.E Gordon’s popular book on engineering *Structures* (1978).

Examining human design can make aspects of animal adaptations more salient: we can learn why the design was successful. One example, again using bats, is the similarity between their wing design and that of sails in Chinese Junks (see Gordon 1978 pp 125-128).

Bat wings and Junk sails both exemplify a very efficient response to balancing structural and aerodynamic factors for wind-based locomotion. A design which emphasizes structural strength may undermine aerodynamism and vice-versa. As Gordon points out, an increase in wind velocity will increase the pressure exerted upon the sail. If the structure in question is too weak, then tensile stresses may result in damage, but a very rigid structure might limit aerodynamism. A sail which is too taut or heavy will not transfer much of the wind’s energy into push.

One solution is to design a sail which is attached to the mast at regular intervals, as in the Chinese Junk. We could “... arrange for the sail to bulge between its supports so that, as the wind pressure increases, the radius of

the curvature diminishes and so the tension force in the canvas remains roughly constant however hard the winds may blow (Ibid, pp 125-126).” We see the same approach in hang gliders: as the wind blows, the ‘sails’ billow between the struts. This design allows the hang glider to maximise aerodynamacy without risking breakage in high winds.

Bat’s wings follow the same engineering principles as Junks and hang-gliders. Their finger bones have evolved into long, thin ‘struts’ which form a framework over which a thin membrane of skin is stretched. As the bat flaps its wings, the tension forces are distributed in the same way as wind across a Junk’s sail. The ingenuity of the design, and the principles upon which it rests, are made salient by reference to man-made objects engineered in response to similar design problems⁴². Bat’s wings and Junk’s sails are analogous.

Principles derived from engineering can play a role in understanding the physical (as opposed to logical) limits of morphospace. An entertaining example, again provided by Gordon (pp 107-109), is the limits on available body size set by the qualities of bone. The idea is that by applying what we know of material strength to bone, we can pick out regularities across all lineages which utilize that material structurally. Biological and artificial analogues play a role by informing and corroborating the engineering model.

One measurement we can make of a material is its *brittleness*. In simple terms (which, in honesty, is the only level at which I can interact with these principles), the brittleness of a material is its tendency to break – for a fracture to develop and cause the structure to split apart. Almost every material will fracture, but these fractures need to be a certain size to actually undermine structure. This length is the ‘Griffith-crack’ and, very importantly for our discussion of bones, for any given material the Griffith-

⁴² Interestingly, Gordon also points out that Pterodactyl wings, which rested on a single ‘strut’, could be understood in terms of the sails of modern yachts.

crack length is absolute, not relative. So a wooden wall which is 10cm thick will have the same Griffith-crack length as a wooden wall which is 1m thick. Once a fracture reaches that length, structural integrity will be undermined as the fracture spreads and the wall splits.

We can use brittleness to understand some of the structural limitations bones impart on terrestrial vertebrates. Because the Griffith-crack length is absolute, the larger an animal becomes and the thicker and longer its bones, the smaller the *relative* crack required to cause a break. In other words, to break a mouse's bones you might need a fracture half the length of the mouse. To break an elephant's bones, you only need a fracture of the same length. But an elephant's bones typically will meet much greater pressures than those of a mouse, simply due to increased weight. So if you drop a mouse its bones will more than likely survive intact. A dropped elephant will crack. This is why, as Gordon puts it, "... elephants need to be very careful; one seldom sees them gambolling or jumping over fences like lambs and dogs (pp108)."

And so the brittleness of bones sets a limit to the size which a terrestrial vertebrate may reach. And this limit may be quantified and tested. Gordon figures that the size of a lion or a man is at about the upper limit of safe size for running and jumping. One way this is supported is through biological analogy: he cites domesticated horses who, through artificial selection, have been bred for dramatically increased size⁴³. Horses break bones frequently, especially compared to smaller Shetlands and donkeys. Horses have been artificially selected for a size which, due to the brittleness of bone, would not be selected naturally. Horses are too sprightly for their

⁴³ I am not completely sure whether we ought to see this as an analogy or a homology. It is homologous insofar as it relates to bones, which are held in horses and other vertebrates due to descent. It is analogous insofar as we are looking at independent evolution events of size increase. It may perhaps be best understood in terms of 'parallel modelling' – due to the homologous constraint of bones, we find similar analogues.

size. Another way of testing this is by taking bone, or synthesizing a relevantly similar material, or simulating bone in a computerized environment, and observing its reaction to different levels of pressure.

Amazingly, these considerations of the tensile strength of bone can give us great inferential reach – even into some aspects of the behaviour of extinct lineages. Larger terrestrial animals would not be sprightly. Like an elephant, they may be able to charge at a fair clip, but they will not be very manoeuvrable. The agile *Tyrannosaurus Rex* from Jurassic Park may be beyond the limits of physical possibility. Apatosaurs, like white men, can't jump.

Analogues are important evidentially for modelling these regularities. They aid in the construction of the model and are crucial to testing it. In the same manner that meerkats and alpine grouse were used to inform the teaching model in the last chapter, machines and technology, given the right circumstances, can also inform adaptive models.

I have illustrated two uses of non-biological analogues. First, they can make nuanced aspects of design more salient, as an examination of the sails of Junks did for bat wings. Second, they can inform models of robust regularities which can ground inferences, as we saw in terms of bones and body-size. Impressively, the application of these regularities to simulations can provide remarkable fine-grained hypotheses about some aspects of the behaviour of extinct lineages⁴⁴. To finish my argument for inferential

⁴⁴ Another way by which our understanding of physical structures can be used to model the past is in the construction of physical models. By 'physical model', I mean the actual construction or simulation of the actual construction of the animal (see Odenbaugh forthcoming for discussion). An arresting example is the interaction between palaeontologists and CGI artists in modern documentaries which attempt to recreate the past, for instance the BBC's *Walking With Dinosaurs*. Here, simulations of the animals were constructed from the skeletal system up, with the proper constraints built in. The task was then to work out how these animals actually moved. These computer simulations actually served to advance scientific knowledge, particularly in regards to the flight of larger pterosaurs (see Francoeur & Segal 2004 for a discussion of the use of computer modelling).

continuity, I will now briefly apply the conditions I set for non-parallel analogies to these artificial cases.

There must be enough analogues to give grounds that Natural Selection does shape phenotype in the way proposed by the model (that it does enough of the causal work)

Non-biological analogies could be very important for this requirement. Compared to biological analogies, where we are restricted by the availability of analogues, in the artificial case we are only limited by our technology and our imagination. So different perturbations can be constructed or simulated and examined – allowing for the careful construction and testing of models.

There must be reasonable grounds for assuming an enabling developmental condition is held across the analogues

As already stated, the developmental condition clause stands in order to ensure that the analogues have the same (or relevantly similar) potentialities or constraints. These can be approximated by the addition of variables and constraints in the model itself. In the case of computer simulations, for example, the computer world can be programmed with a particular physics and agents can be modified according to the limitations of their real-world targets (see note 5).

EITHER,

There must be other streams of data which can corroborate the hypothesis for the explanatory target, gaining the causal depth required for warrant

I see this clause working in exactly the same fashion for both biological and artificial analogues. Both can be part of an integrated solution.

OR,

There must be enough information across the analogues to allow us to increase specificity by bootstrapping.

This statement could almost be taken as a *description* of the modelling process. A solution is arrived at by examining different perturbations of the model, and adjusting the variables towards the required target given those results.

And so, when we are judging the epistemic warrant of an artificial system which is fulfilling an analogous role, we should make this judgement based upon these criteria. We should ensure that we have examined enough perturbations of the model. We should ensure that it picks out the right dimensions of variability and initial condition which reflect the potentiality or constraint of the target system. We can see the model as part of an integrated solution. If it stands alone, there must be enough perturbations examined to provide the necessary variability.

In conclusion, I have shown that the concept of ‘analogy’ as described in the first seven chapters, and the criteria I have given for judging its epistemic warrant, is applicable in other realms. The use of analogies from material sciences like engineering, and abstract models and computer simulations, can fulfil the same role as biological analogies. The sceptical problems they face are not different in kind from those faced by cases of convergent evolution. So although I have focused on the limits of these inferences, the application of both ingenuity and a further understanding of the natural world can expand these limits.

Conclusion

Upon sighting the platypus, Shaw suspected that a duck's bill and webbed feet had been sewn onto a mammal pelt. Given the clear categories provided by Aristotelian theory, a mammal having avian features is a surprise. In an evolutionary light, however, there should be no surprise. Given the effect of Natural Selection on phenotype, and given the similarities between niches occupied by disparate lineages, we should *expect* to find animals which have evolved similar adaptations.

Given evolutionary theory, we should also expect closely related lineages to have similar traits. They have inherited a similar developmental system from a common ancestor. This is what makes outlier lineages surprising. For example, the platypus has two startling outlier traits. Males have a venomous spur on their hind legs. Venom is extraordinarily rare in mammals, but fairly common in reptiles and insects (Whittington et al 2008). Platypus (and echidna) also use *electroreception* (Pettigrew 1999). Platypus hunt small invertebrates by detecting the electrical currents they generate.

The main theme of this thesis has been how we can use similarities like that between duck and platypus feet to inform us about discrepancies like that between platypus and typical mammal sensory apparatus.

To conclude I want to reemphasize what I see as the important lessons from the previous chapters. I would like to think that I have made arguments which have important consequences for both philosophers and scientists, so I will discuss each in turn.

Scientific work which attempts to retrodict lineages using homology and analogy must keep the particular roles they play clearly delineated. If a resemblance is due to descent, then comparative information can play two

roles: it can be used to inform us about the conditions of the past and it can, when contrasted with some adaptive model or final condition, help hypothesize difference-makers. If a resemblance is due to continuity of niche, then its most obvious role is in informing us about the relationship between the trait we are interested in and environmental variables. I have mostly explored these roles in their application to the retrodiction of outlier lineages

There is reason to be sceptical of many homologous claims about outlier lineages, including our own. Because our clade is impoverished, and many of the traits we are interested in are particularly labile, the probability we should attach to some homologous inferences is worryingly low. For example, if we wish to know whether our ancestors were patrilocal like chimpanzees and bonobos or matrilocal like many other primates, the lability of dispersal strategies in primates weakens our commitment to developmental entrenchment. The scarcity of data-points weakens cladistic parsimony. Without independence evidence I would be wary of committing to either picture. For a labile trait, discovering a relationship between our target and some environment or physiological factor (as we saw in parallel modelling) is a better method.

In the application of analogues, as well, it is important to ensure that we findings are supported by the right kind of data. If an analogue is a central to a theory, just citing the example is not sufficient. We must also look at corroborating evidence for the model we have constructed. We must especially look for falsifying cases: our adaptive model will specify a particular trait's relationship with an environment, so if we discover an environment without the trait this gives us an important opportunity to refine the model.

In general, comparative biological data (and, as I have suggested in the coda, non-biological data) can provide a rich data-stream for the construction and testing of hypotheses. In the case of analogies, scientists should shift from half-heartedly implying convergences to attempting to

properly incorporate them into their theories.

I have put emphasis on a *synthesized* approach to biological explanation. When explaining an aspect of phenotype we must pay attention to the roles of both Natural Selection and Developmental Resources (as well, of course, of other non-selective processes such as drift).

Philosophically I have tended to avoid hard and fast definitions of some concepts in the explanatory tool-kit of evolutionary biology. In some quarters this kind of approach is becoming more popular (see, for instance, Godfrey-Smith's (2009) multi-dimensional definition of a Darwinian Population), and rightly so. Biological phenomena are complex and often stochastic, so I don't think we should expect our concepts to be clearly differentiated. It is frequently the case that biological categories are best viewed in terms of continua, so having flexible conceptual tools is an advantage.

I have also emphasized (though not argued for) ecumenism about explanation. Leaving metaphysical questions aside, given the complexity of nature and our comparatively impoverished epistemic status, the utilization of many explanatory strategies and approaches should not be viewed negatively. There are many kinds of questions we can ask about biological phenomena, and correspondingly many kinds of explanations which can be justifiably applied to them.

Although I have focused on just one possible data-stream available for evolutionary biology as an historical science, I hope it has been made clear that the main strength of historical explanations lies in their ability to incorporate many data streams. Even if we have doubts about the consilience of various sciences in terms of causation – we should have none about their explanatory consilience.

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