20 Narrative Solutions to a Common Evolutionary Problem

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Abstract
To give a Darwinian explanation of the traits of a species, it is not enough to show that the traits are appropriate for the environments inhabited. One must also show that the traits in question are more appropriate than the (presumed) ancestral traits from which they are derived. But one must go further still. Even if there is no question that the derived traits are more appropriate, one must still specify the sequence of modifications leading from the ancestral to the derived traits, each step of which is fitness-enhancing. How better – indeed, how else – than by a narrative? I illustrate these points through the evolution of flatfish eyes. This is part of an ongoing project concerning what narratives are good for, what narratives do better than non-narrative arguments: in short, why we need narratives.

20.1 Introduction

Sometimes, in order to understand an occurrence, we need to know what happened prior to that. (Yes, that sounds obvious, and yet . . . .)

And sometimes it’s not enough to know what happened immediately prior to that. We need a *backstory* that rewinds time to some event in the more distant past, and then takes us forward through events that (1) were not foreseeable from the starting point, and (2) were consequential for the outcome of interest, (3) in the order in which they occurred and not just any order. Such a backstory is *narrative-worthy* – a narrative is just right for the occasion – as I will explain later.

I’ll illustrate these points with a common problem from evolutionary biology. Or rather, I’ll rely on the common problem in order to introduce/motivate the need for a narrative solution. Evolutionary explanations sometimes (often?) invoke only circumstances contemporaneous with the phenomena to be explained – no backstory, indeed, *atemporal* evolutionary reasoning, as odd as that may sound. This might be satisfactory in some contexts. But it is not satisfactory in other contexts, like those I’ll discuss, where narrative-worthy backstories are called for.

20.2 Darwinian Assumptions: Successive, Slight Modifications

Flatfishes – halibut, turbot, sole, others – live horizontally/flat on the sea floor. They differ from vertical fishes in appropriate ways. Most notably, instead of having one eye on each side of their head, they have both eyes on one side, the topside, making it easier to see their prey and watch out for predators. Flatfishes are commonly coloured in a way that camouflages them against their background. Usually, just the topside is camouflaged; the unseen bottom is pigmentless (Figures 20.1 and 20.2).

It is common to account for the traits of a species – like the lifestyle, anatomy and coloration of flatfishes – in terms of their appropriateness, the ways in which they individually, and in combination, enhance the fitness of their possessors. The possession of fitness-enhancing traits is what we expect from evolution by natural selection.

This kind of reasoning is odd, though, when you think about it: it amounts to an evolutionary account of the present that does not invoke the past, just prevailing circumstances. It's an atemporal evolutionary account.

It's a common enough manner of reasoning to have been called out for criticism by Stephen Gould and Richard Lewontin (1979). They dubbed it the 'Panglossian paradigm', after Voltaire's Dr. Pangloss, for whom everything in

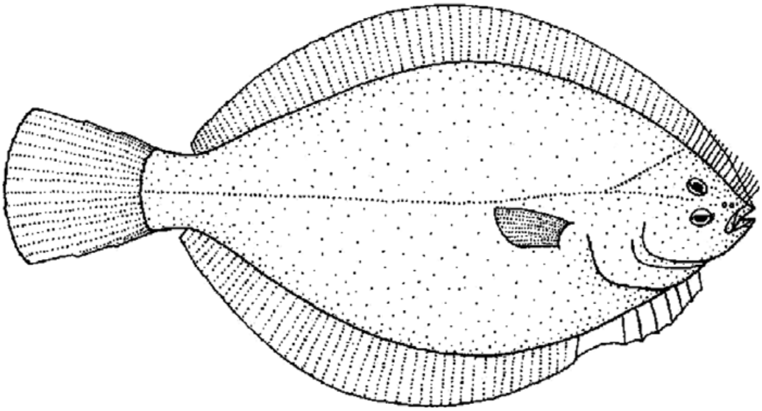

Figure 20.1 **Flatfish (flounder) topside**
Rhombosolea leporina (Yellowbelly flounder)
Source: This illustration is licensed under the Creative Commons Attribution ShareAlike 1.0 license. The author is Dr Tony Ayling. The illustration was originally published in Tony Ayling and Geoffrey Cox, *Guide to the Sea Fishes of New Zealand* (Auckland: William Collins Publishers, 1982) https://commons.wikimedia.org/wiki/File:Rhombosolea_leporina_(Yellowbelly_flounder).gif.

Figure 20.2 **Still life by Jan van Kessel the Elder**
Jan van Kessel the Elder, 1626–79.
Source: Wikimedia Commons.

the world was maximally appropriate. Thus, species are maximally adapted to their environments. But, to account for the traits of species entirely in terms of their '*current* utility', Gould and Lewontin objected, is to pretend that adaptation does not take time. Such accounts reflect the untenable assumption of '*immediate* adaptation' to whatever environment a species inhabits, the '*immediate* work of natural selection'.[1]

Surely the targets of Gould and Lewontin's critique did not really believe that species instantaneously adapt to their environments. But perhaps they assumed, along with John Maynard Smith, that 'most populations have had time to come close to the *optimum* for the environment in which they live' (Maynard Smith 1993: 11–12; my emphasis; but see also Maynard Smith et al. 1985). Had there been *in*sufficient time for populations to 'come close to the optimum for the environment in which they live', then one could not make sense of their traits without taking into consideration the ancestral starting points from which they had not completely departed. But, as it (supposedly) happens, there's no need to bother with the past; the present is enough.

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[1] Olmos (Chapter 21) unpacks the logic of Gould and Lewontin's argument in detail, finding that their criticisms do not bear only on the narrative nature of adaptationist accounts, but on other aspects of them as well.

On the Panglossian paradigm, there is another, related respect in which history is irrelevant. It has to do with the equilibrating character of an optimizing process like evolution by natural selection – or, rather, as evolution by natural selection is commonly conceived. Consider an analogy. We find a marble lying in the bottom of a bowl. How did this come about? We need only take into account the prevailing properties of the marble and the bowl, and the principles that govern this mini-universe. The past is largely irrelevant, since the marble would have rolled around and eventually come to rest there, no matter where it started. Similarly, one might think that a species (marble) evolves by natural selection in its environment (bowl) until it attains *the* optimum combination of traits, the equilibrium point where it then rests, no matter its starting point. One need only take into account the prevailing circumstances.

Darwin himself could not have reasoned persuasively in this manner. His case for evolution by natural selection vs special creation depended on linking the present to the past. For instance, it makes better sense to attribute imperfect but satisfactory traits – like the wonky but workable placement of flatfish eyes – to the trial and error modification of an imagined ancestor, in this case with an eye on each side, than to an all-knowing and benevolent creator who engineers each species from scratch.

Evolutionary biologists today are rarely concerned to dispatch special creation. But, insofar as they are *Darwinians*, they have other sceptics to contend with, and in doing so they have other reasons for looking beyond the present into the past. And here's (at least one reason) why.

To make sense of the traits of a species, a Darwinian should be able to go back in time to an ancestor of that species, and then forward to the species in question. But, in going forward from the ancestor, the good Darwinian cannot rely on an all-at-once modification. It should be possible to specify a *sequence of slight modifications* that would lead to the descendant. As Darwin acknowledged:

> If it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down. (Darwin 1859: 189)

I would just add the following friendly amendment (this is after all what he meant):

> If it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous, successive, slight modifications, *each of which increases fitness*, my theory would absolutely break down.

There are times when Darwinians do not hold themselves – and are not held – to these standards, presumably on the grounds that the ancestral and gradual intermediate stages of evolution are not difficult to fathom and are perhaps not worth the worry. But there are also cases where it is not at all clear that there is a backstory that meets these standards, and the challenge is to provide one.

20.3 Plausible Orderings of Modifications

St. George Jackson Mivart, for one, challenged Darwin on his own terms (Mivart 1871).[2] And flatfish eyes (among other examples, see further) served him well in this regard. To give a Darwinian account of their eyes, by Darwin's own criteria, it is not sufficient to demonstrate the usefulness of that arrangement at present. One must also propose a sequence of slight modifications leading from an ancestor with one eye on each side to descendants with both eyes on one side, each step of which increases fitness.

What's a plausible sequence? Surely not by slight displacements of one eye *through* the skull to the other side! Surely it would involve slight displacements of one eye *over the top* of the skull to the other side. But that leaves unanswered how the initial and early displacements could have been fitness enhancing. He imagines a fish lying flat on its side with one eye in the sand. What's the advantage of having the lower eye only slightly closer to the top of the skull? It's still in the sand. How can the initial migrations of the eye have been anything but injurious, given the skull/eye-socket reconstructions involved?

> Another instance which may be cited is the asymmetrical condition of the heads of the flatfishes (Pleuronectidæ), such as the sole, the flounder, the brill, the turbot, &c. In all these fishes the two eyes, which in the young are situated as usual one on each side, come to be placed, in the adult, both on the same side of the head. If this condition had appeared at once, if in the hypothetically fortunate common ancestor of these fishes an eye had suddenly become thus transferred, then the perpetuation of such a transformation by the action of 'Natural Selection' is conceivable enough. Such sudden changes, however, are not those favoured by the Darwinian theory [. . .] But if this is not so, if the transit was gradual, then how such transit of one eye a minute fraction of the journey towards the other side of the head could benefit the individual is indeed far from clear. It seems, even, that such an incipient transformation must rather have been injurious. (Mivart 1871: 37–38)

Mivart generalized the problem and gave it a name: 'the incompetency of "natural selection" to account for the incipient stages of [ultimately] useful structures' (Mivart 1871: 23). It has since been shortened to 'the problem of incipient stages'.[3] As he put the point:

> 'Natural Selection,' simply and by itself, is potent to explain the maintenance or the further extension and development of favourable variations, which are at once

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[2] A nice introduction to Mivart's challenge and the evolution of flatfish eye placement is Zimmer (2008).

[3] In his work on the evolution of leaf mimicry in butterflies, Suzuki (2017) includes updates on most of the problematic cases of incipient stages that Mivart raised, including flatfishes.

> sufficiently considerable to be useful from the first to the individual possessing them. But Natural Selection utterly fails to account for the conservation and development of the minute and rudimentary beginnings, the slight and infinitesimal commencements of structures, however useful those structures may afterward become. (Mivart 1871: 23)

In addition to flatfish eyes, he illustrated the problem with other traits like the giraffe's neck, vertebrate limbs and mimicry. And mammary glands:

> Is it conceivable that the young of any animal was ever saved from destruction by accidentally sucking a drop of scarcely nutritious fluid from an accidentally hypertrophied cutaneous gland of its mother? (Mivart 1871: 47)

For these and other reasons, Mivart inferred that new species arise not gradually, but with 'suddenness'.

> Not only are there good reasons against the acceptance of the exclusive operation of 'Natural Selection' as the one means of specific origination, but there are difficulties in the way of accounting for such origination by the sole action of modifications which are infinitesimal and minute, whether fortuitous or not.
>
> Arguments may yet be advanced in favour of the view that new species have from time to time manifested themselves with suddenness, and by modifications appearing at once [. . .] the species remaining stable in the intervals of such modifications. (Mivart 1871: 97)

Darwin well understood and appreciated the difficulty that Mivart had raised, and in the 6th and final edition of *On the Origin of Species* he devoted considerable space to the problem. Referring to this and other criticisms, Darwin wrote:

> A distinguished zoologist, Mr. St. George Mivart, has recently collected all the objections which have ever been advanced by myself and others against the theory of natural selection, as propounded by Mr. Wallace and myself, and has illustrated them with admirable art and force. When thus marshalled, they make a formidable array. (Darwin 1872: 176)

Darwin responded to a variety of Mivart's objections. But he took most seriously, and spent the most time responding to, the problem of incipient stages (1872: 177–190), including a solution to the problem of flatfish eyes. He affirmed that the trajectory of evolution involved the eye moving over the top of the skull, onto the other side. The maturation of flatfishes provided the evidence. According to August Malm (1867), flatfish larvae swim vertically and – appropriately under the circumstances – have one eye on each side of their head. But, as they develop, one eye begins to migrate towards and then over the top of the skull, to the side that becomes the topside of the horizontal, bottom-dwelling adult, as shown in the sequence in Figure 20.3. The migration of the eye during the development of individual flatfishes, together with their

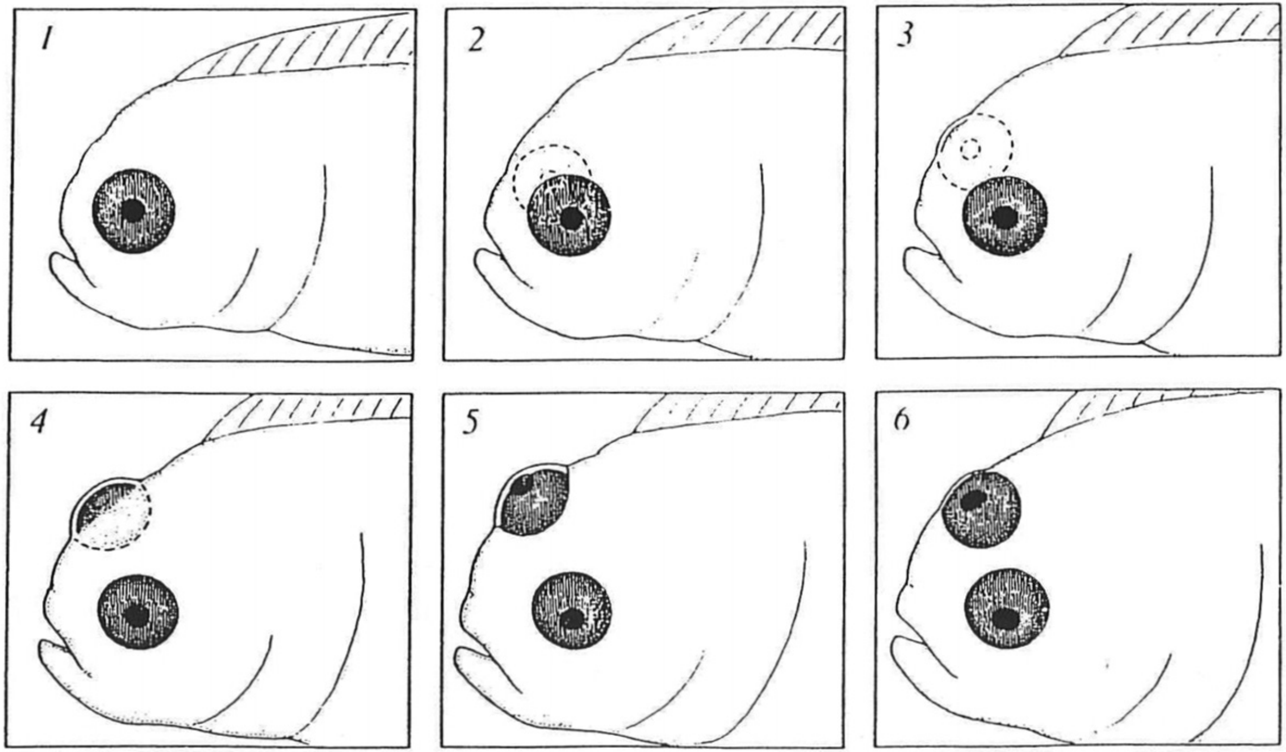

Figure 20.3 **A depiction of eye migration in starry flounder larvae, that also illustrates Darwin’s suggested evolutionary account of the flatfish eye.**

Source: Policansky (1982).

change in orientation from vertical to horizontal, reflects the trajectory of their evolution. Why else would flatfishes undergo that course of development, other than because they were descendants of vertical, symmetrically eyed fishes?

But that leaves unanswered how the initial migration of the one eye, and early extensions of that migration, could have been fitness-enhancing, which had been Mivart's main puzzle. Darwin didn't entirely capitulate on this, but partly/largely. He attributed the initial, slight migration of the eye, and then early extensions of that migration, not to evolution by natural selection, but rather to Lamarckian inheritance of acquired characters. He took it on authority from Malm that very young flatfishes lying on their sides on the sea floor, before eye migration is complete, strain to see with their bottom eye

> [. . .] and they do this so vigorously that they eye is pressed hard against the upper part of the orbit [socket]. The forehead between the eyes consequently becomes, as could be plainly seen, temporarily contracted in breadth. (Darwin 1872: 187)

Suppose this forced displacement of the eye, so as to see better, was inherited by the next generation, who also strained to see. Resulting in still further displacement of their eyes. The further, forced displacement was also inherited. This took place generation after generation until the eye made its way far enough around the skull that it was sufficiently out of the sand, at which point its migration to the other side was maintained and extended to the present state by natural selection. It was a largely Lamarckian, only partly Darwinian solution.

> We thus see that the first stages of the transit of the eye from one side of the head to the other, which Mr. Mivart considers would be injurious, may be attributed to the habit, no doubt beneficial to the individual and to the species, of endeavouring to look upwards with both eyes, whilst resting on one side at the bottom. We may also attribute to the inherited effects of use the fact of the mouth in several kinds of flat-fish being bent towards the lower surface. (Darwin 1872: 187–188)

Darwin further explained the lack of pigment on the bottom of flatfishes in terms of the Lamarckian notion that disuse of a trait, over many generations, leads to its loss (Darwin 1872: 188).

Somewhat tangentially, Lamarck had offered his own explanation of flatfish eye placement. The ancestors of flatfishes fed in very shallow waters along shorelines, he supposed, waters so shallow that they had to lie flat on their sides. '[T]his requirement has forced one of their eyes to undergo a sort of displacement, and to assume the very remarkable position found in the soles, turbots, dabs, etc.' (Lamarck 1914: 120).

The all-at-once modification, as applied to flatfish evolution, and many other problematic cases, was developed in great detail by Richard Goldschmidt (1940) and had considerable influence well into the twentieth century and, in one form or another, to this day. Here is a thin version of his thinking, in connection with flatfish eyes:

> In a former paper (Goldschmidt 1933) I used the term 'hopeful monster' to express the idea that mutants producing monstrosities may have played a considerable role in macroevolution. A monstrosity appearing in a single genetic step might permit the occupation of a new environmental niche and thus produce a new type in one step [. . .]. A fish undergoing a mutation which made for a distortion of the skull carrying both eyes to one side of the body is a monster. The same mutant in a much compressed form of fish living near the bottom of the sea produced a hopeful monster, as it enabled the species to take to the life upon the sandy bottom of the ocean, as exemplified by the flounders. (Goldschmidt 1940: 390–391; and see 1933: 545)

The question of flatfish eyes is often posed as one that pits a Goldschmidtian (and, to be fair, Mivart-inspired) solution against a Darwinian approach – for example, in Thomas Frazzetta's (2012) review: 'Flatfishes, Turtles, and Bolyerine Snakes: Evolution by Small Steps or Large, or Both?'.

The problem of flatfish eyes, from a Darwinian point of view, seems to have eluded even the master Darwinian communicator, Richard Dawkins. No, Dawkins doesn't go Lamarckian, nor Goldschmidtian. But he pulls up short of going fully Darwinian. He makes the Darwinian point that it is more reasonable to attribute asymmetric flatfish eyes to the modification of a symmetrically eyed ancestor than to special creation. Surely an intelligent designer would have created flatfishes more in the manner of skates and rays, flattened from top to bottom, with both eyes on top, rather than flattened from side to side and requiring the migration of one eye to the other side.

> Even though its [the flatfish's] evolutionary course was eventually destined to lead it into the complicated and probably costly distortions involved in having two eyes on one side, even though the skate way of being a flat fish might *ultimately* have been the best design for bony fish too, the would-be intermediates that set out along this evolutionary pathway apparently did less well in the short term than their rivals lying on their side. (Dawkins 1986: 92–93)

Yes, 'apparently' in the lineages that beget flatfishes, lying flat on one side with a migrating eye prevailed over flattening from top to bottom. But how could the admittedly 'complicated and probably costly distortions' of the intermediate stages have been sufficiently advantageous to be selected for?

Interestingly, there have been recent – for the first time – fossil findings of flatfishes with intermediate stages of eye migration (Friedman 2008). But there is still no generally accepted, functional account of the fitness contributions of the early steps. The most promising clue is a fact about some flatfishes, maybe many or all, that has been known for quite a long time although not considered until recently in this connection (Olla, Wicklund and Wilk 1969; Stickney, White and Miller 1973; Friedman 2008: 211; Frazzetta 2012: 33). That is, adult flatfish (flounders in this case) sometimes use their dorsal and anal fins (what would have been the top and bottom fins in their ancestors but are right- and left-side fins in flounders) to prop themselves up, raising their heads to better see above them and lunge at their prey.

Now if early flatfishes could raise their heads in this way, and in the process raise their lower eyes out of the sand, then a slight migration of the lower eye could have allowed slightly better vision than having it face straight down and may have been selected for. And a further extension of the migration would be advantageous and selected for. And so on and so on, the entire eye migration thus being due to evolution by natural selection.

The sequence here is crucial. Head elevation for lunging is not only adaptive in combination with other flatfish traits. Its position in the sequence of evolutionary events, prior to eye migration, is what makes eye migration adaptive and hence evolutionarily possible.

An account of flatfish eye placement in terms of its current usefulness is not wrong, but it is possibly misleading, and in any case sorely incomplete, prompting the sort of objection raised by Mivart. A Darwinian explanation requires a backstory – back to an ancestor that had symmetrically placed eyes; and then forward from there, through a careful – just the right, so to speak – sequence of stages.

The problem of incipient stages – requiring a backstory – arises for various reasons. In the case of flatfish eye migration, it has to do with so-called ‘epistatic’ interactions, where the fitness contribution of a trait depends on the presence or absence of other traits. In the case of ‘sign epistasis’, the fitness contribution of a trait is positive or negative (plus ‘sign’ or minus ‘sign’) or zero depending on the presence or absence of another trait (Weinrich, Watson and Chao 2005; Weinrich et al. 2006; Poelwijk et al. 2007). For example, eye migration is fitness-enhancing in combination with head elevation, but fitness-neutral, or more likely fitness-diminishing alone. This particular kind of epistatic interaction results in there being multiple, sequential pathways to an optimal outcome, some of which are traversable by natural selection and some not. Which is to say, again, that it is not enough to attribute even highly adaptive traits to natural selection without also positing an ancestor and a carefully sequenced route from the ancestor to the descendant in question.

Consider another example of the problem of incipient stages that also points to the importance of backstory, but that arises and is resolved in a different way – different from the epistasis case. It concerns the evolution of wings. Mivart is often said to have asked ‘What use is half a wing?’ Mivart did not say that (at least not in the text regularly cited), and that does not sound like his manner of posing the more general problem. Stephen Gould (1991) had a better way of putting Mivart’s point: the

'5 percent of a wing' problem. How could evolution by natural selection of slight modifications lead from wingless, flightless ancestors to winged, flying descendants? How could the miniscule, incipient wing-lets have been sufficiently useful for flying in order to be favoured by natural selection? Mivart concluded, 'It is difficult [...] to believe that the Avian limb was developed in any other way than by a comparatively sudden modification of a marked and important kind' (1871: 107). Which, again, violates Darwin's 'successive, slight modifications' constraint.

The most promising solution in this case is one that Darwin himself proposed, and illustrated with the case of wings.[4] The basic idea is that the incipient stages of the trait in question were useful in a (perhaps very different) way than the later stages. 'In considering transitions of organs, it is so important to bear in mind the probability of conversion from one function to another' (Darwin 1872: 183).

The structures that were eventually modified for flight might have served a variety of other functions, depending on the animal in question (e.g., insects vs birds) and depending on issues of scale. Darwin himself suggested that the thoracic wings of some insects might be modifications of parts originally related to respiration. Wings of insects and birds might, in their incipient stages, have served a variety of aerodynamic uses other than flight, like gliding and altitude control during descent. Narratives of the evolution of bird flight generally begin with the modification of four-legged ancestors into bipedal descendants, followed by modification of the forelimbs into wings. On some accounts, the initial modifications improved running and jumping (e.g., by improving balance). On other accounts, the modification followed tree climbing, and served aerodynamic uses related to descent mentioned above.

20.4 When Narratives Are Worthwhile

The evolution of flatfish eyes, wings and many other traits are narrative-worthy, in a sense I'll now explain. But first: I'm going to rely on a fairly minimal view of narratives, namely that they relate what happened, one event at a time. In this regard I'm following the lead of narrative theorists who adopt similarly minimal views of what counts as a narrative and who

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[4] Gould 1991 and Brandon 1990 are nice analyses of the issues involved in the stepwise evolution of wings. Both focus on the now-classic work of Kingsolver and Koehl (1985; see also 1994) on the evolution of insect wings. Gould puts it in the context of Mivart's problem of incipient stages, and Darwin's solution of functional shift, while Brandon uses it to illustrate the character of explanations. Garner, Taylor and Thomas (1999) includes a useful presentation of the main theories of the evolution of avian flight and the sequences of trait acquisition that the alternative theories require.

concede that almost anything is narratable, but who deny that everything narratable is worth narrating. Some narratives are pointless. As William Labov famously commented:

> Pointless stories are met (in English) with the withering rejoinder, ‘So what?’ Every good narrator is continually warding off this question; when his narrative is over, it should be unthinkable for a bystander to say, ‘So what?’
>
> There are a great many ways in which the point of a narrative can be conveyed – in which the speaker signals to the listener why he is telling it. To identify the evaluative portion of a narrative, it is necessary to know why this narrative – or any narrative – is felt to be tellable. (Labov 1972: 366, 370)

Labov’s term ‘tellable’ has become the state of the art (narrative theory) term for what I prefer to call narrative-worthy. But I like his term ‘pointless stories’. What is a narrative-worthy as opposed to a pointless story? The criteria that I offer may just be a few of many criteria for narrative-worthiness. Perhaps there are stories worth narrating that do not meet the following criteria but are worth telling for other reasons.

For starters, I’d say narratives are good for situations where we don’t know – on the basis of what has already happened, and general principles – what will happen subsequently, and we need to be told.[5]

To clarify, this does not render pointless all of those stories where the narrator begins with the ending. Most historical narratives, in both civil history and natural history, begin with the outcome, and the narrator then proceeds to tell how it came about. Rather, the criterion calls into question the need for narrating how an outcome came about, when the outcome was already foreseeable from the initial events.[6]

An example of a situation where narratives are not particularly useful – where they do not serve this basic function – involves equilibrating/optimizing processes like the one discussed earlier of a marble coming to rest in the bottom of a bowl. Why narrate its trajectory – ‘it was there, then it was there, then there’ – if we can derive from the start where the marble will end up? And regardless of where it started from.

Similarly, why narrate the evolution of a species in an environment if we ‘know’/suppose that it will eventually reach its predictable optimal state given that environment. And regardless of where it started from?

Whereas to make sense of flatfish eyes, wings, etc. in terms of evolution by natural selection, one must provide a backstory – back to a presumed ancestor, and then the sequence of stages moving forward. And these stages were hardly guaranteed by what preceded them. They could hardly be derived from past

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[5] Crasnow (Chapter 11), links such narrative-worthiness to the work of tracing and casing.

[6] Andersen (Chapter 19), uses the notion of ‘scripts’ to argue that mathematicians skip precisely such foreseeable sequences when reading mathematical proofs.

circumstances. Flatfish head elevation was hardly foreseeable from the point at which their ancestors first lay flat on their sides on the sea floor. It was certainly not foreseeable by generations of naturalists who contemplated the evolution of flatfish eye placement. Nor, if one were to start the backstory earlier (as I'll discuss shortly) would it be predictable that predatory fishes inhabiting the sea floor would adopt the behaviour of lying flat on their sides, given that many bottom-dwelling predators (e.g., groupers) never have.

Consider the prominence of narratives in Darwin's work, and what makes them so worthwhile. Their employment, and their value reflect in part Darwin's view that, outside of gradual adaptation to environmental circumstances, there is nothing inevitable in the history of life.

> I believe in no fixed law of development, causing all the inhabitants of a country to change abruptly, or simultaneously, or to an equal degree. The process of modification must be extremely slow. The variability of each species is quite independent of that of all others. Whether such variability be taken advantage of by natural selection, and whether the variations be accumulated to a greater or lesser amount, thus causing a greater or lesser amount of modification in the varying species, depends on many complex contingencies, – on the variability being of a beneficial nature, on the power of intercrossing, on the rate of breeding, on the slowly changing physical conditions of the country, and more especially on the nature of the other inhabitants with which the varying species comes into competition. (Darwin 1859: 314)

> [I]f we must marvel, let it be at our presumption in imagining for a moment that we understand the many complex contingencies, on which the existence of each species depends. (Darwin 1859: 322)

These 'many', unforeseeable 'complex contingencies' need to be added to each evolutionary narrative, in the order they arise.

So, again, a good occasion for a narrative is when we don't know what will happen next and need to be told. But that still leaves room for a lot of narratives not worth telling, pointless. The events worth including are not just those that we would not have foreseen otherwise. They should also be consequential. Otherwise what is the point of including them in the narrative?

Note that, in the last of the Darwin quotes above, he refers not only to the 'many complex contingencies' that arise in the course of the evolution of each species, but those contingencies 'on which the existence of each species depends', i.e., which are consequential for the evolution of each species. These two facts about evolutionary history correspond to two reasons why narratives are so appropriate for making sense of evolutionary outcomes: the unpredictability of the events narrated, and their consequential character.[7]

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[7] Elsewhere (Beatty 2006; 2016; 2017), I have discussed these two criteria of narrative-worthiness in terms of the events narrated being *contingent* (or *contingent* per se) – unpredictable, matters of chance – and in terms of the narrative outcome being *contingent upon* – dependent upon – those

Philosopher of history William Gallie stressed the importance of the two criteria in his reader-centric view of what makes a narrative 'worth following'. In the first paragraph below he stresses the otherwise unpredictable elements that we rely on narratives to supply. In the second paragraph, he stresses that the events in a worthwhile narrative are consequential for the outcome.[8] Generally, in narratives,

> [. . .] there is a dominant sense of alternative possibilities: events in train are felt to admit of different possible outcomes – particularly those events that count [. . .] that deserve to be recorded, that could be the pivot of a good story. [. . .] [S]ide by side with this there is the recognition that many events, or aspects of events, are predictable either exactly or approximately. But, although recognised, this predictable aspect of life is, so to speak, recessive or in shadow. It is in contrast to the generally recognised realm of predictable uniformities that the unpredictable developments of a story stand out, as worth making a story of, and as worth following. [Or, in other words, using the terminology of footnote 7 (which I said I was trying to avoid, but I just can't help myself), the *contingent* (or *contingent* per se) developments are 'worth making a story of'.]
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> [O]f [still] greater importance for stories than the predictability relation between events is the converse relation which enables us to see, not indeed that some earlier event necessitated a later one, but that a later event required, as its necessary condition [i.e., that it was *contingent upon*], some earlier one. (Gallie 1964: 26; my emphasis)

I like to represent these two features of narrative-worthy stories with a branching tree of possibilities (Figure 20.4). In this world, the occurrence of event A leaves open the possibility of either B1 or B2. The occurrence of B1 leaves open the possibility of either O1 or O2 and forecloses the possibility of B2 and along with it O3 and O4. A–B1–O2 is one possible history in this world, A–B2–O4 another. There are multiple possible histories in this world; only one can come to pass.

Let's say it was A–B1–02. B1 was not derivable from A; B2 might have occurred instead. Moreover, B1 was consequential – it made a difference; had B2 occurred instead, 02 would not have occurred. In the literature on narrative theory, events like B1 are often referred to as turning points or branch points (Beatty 2016: 36–37 and references therein). As far as evolutionary narratives are concerned, 'A' stands for the ancestral state with which the backstory begins, and the 'O's' stand for alternative evolutionary outcomes.

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events. I have focused on those two uses of the term 'contingent', and the significant differences between them, because the terminology is ubiquitous in the biological literature, and because the two uses can be and are conflated. This point has been pretty well received; Griffiths (Chapter 7) uses it to articulate the differences between the Darwins' plant research and that of Julius Sachs. Nonetheless, here I am trying to see what good or ill comes from dropping that terminology in favour of the language I have substituted in the text above.

[8] Hajek (Chapter 2) proposes, by contrast, that the consequence of events in scientific narratives can also derive from meta-diegetic considerations.

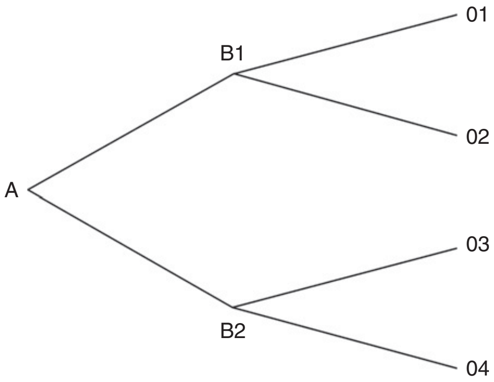

Figure 20.4 **Branching-tree representation of narrative-worthy stories**

The diagram helps to show how the sequence A–B1–O2 counts as an explanation of O2 on the prominent ‘counterfactual difference-making’ conception of explanation. As James Woodward expresses the basic idea:

> An explanation ought to be such that it enables us to see what sort of difference it would have made for the explanandum if the factors cited in the explanans had been different in various possible ways (Woodward 2003: 11)
>
> [A] common element in many forms of explanation, both causal and non-causal, is that they must answer what-if-things-had-been-different questions. (Woodward 2003: 221)

The occurrence of B1 helps to explain O2, in the sense that, had B1 not occurred (had B2 occurred instead), then O2 would not have resulted. Whether B1 or B2 occurs makes a difference.

There is a case to be made that worthwhile narratives include, at least implicitly, what did not occur as well as what did, at least some of the counterfactual as well as the factual sequences of events. But I won’t press that case here (see Beatty 2016; 2017). At the very least, to see the worth of a narrative is to consider what did not happen and thereby see that there were consequential turning points, which, again, contributes to the explanatory character of the narrative.

Figure 20.5 shows a branching time representation of flatfish evolution. The acquisition of head elevation is a turning point that was not inevitable given past events, and that was consequential for the outcome. The order of events here is crucial. It is not enough to consider the three traits in question purely contemporaneously. Yes, they work well together, but that does not explain their presence. The acquisition of the trait, lying flat, made possible the evolution of head elevation for lunging, which in turn made possible the evolution of eye migration.

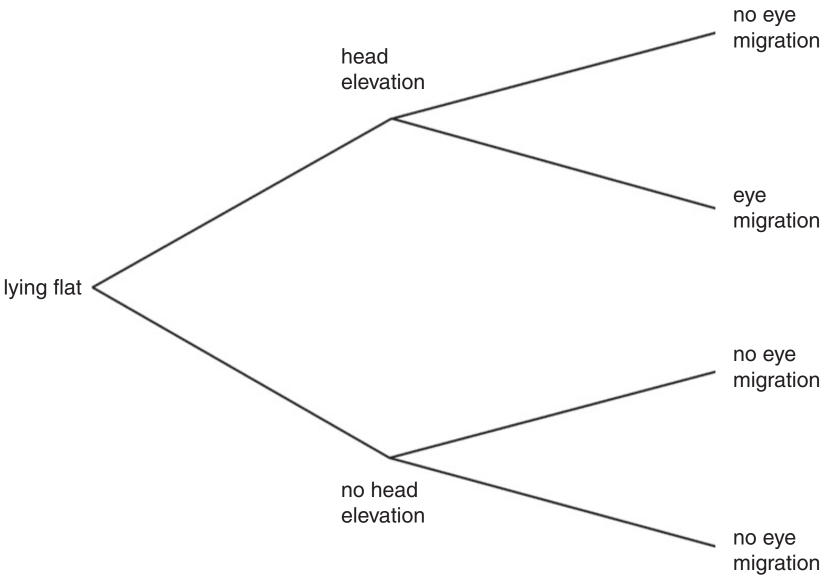

Figure 20.5 **Branching time representation of flatfish evolution**

20.5 Conclusion

In order to understand an occurrence, we sometimes need a backstory that rewinds time to some event in the more distant past, and then takes us forward through events that (1) were not foreseeable from the starting point, and (2) were consequential for the outcome of interest, (3) in the order in which they occurred and not just any order. We need a backstory that is narrative-worthy in these respects. Such a backstory is explanatory.

I'll end with a question that may have occurred to you already, namely how far back should the backstory go? I'm not sure there is a definitive answer to this. But surely it depends in part on the question being asked, or what counts as puzzling.

Gerd von Wahlert rewound the flatfish evolution clock back beyond their ancestors' horizontal lifestyle – the point at which the narratives above begin – to their more distant ancestors' vertical lifestyle. According to his narrative, the ancestors then evolved to rest/'sleep' lying flat. (Yes, some fishes rest/sleep on their sides.)[9] And subsequently evolved a horizontal lifestyle. He proposed this

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[9] Aquarium owners may be familiar with the 'beds' or 'hammocks' or 'pads' that can be attached to the glass so that they can see their pet 'betta' fish napping, often lying on their sides.

as a solution to the puzzle of flatfish eye placement, and a way to avoid Goldschmidt's hopeful monster scenario.

> The flatfish are usually cited not only as a paradigm of adaptation to benthonic life but frequently as a case of an unexplainable major evolutionary step; they are referred to by Goldschmidt as owing their origin to a 'hopeful monster'. Analysis of their structure and their habits has, however, revealed a simpler story (Wahlert 1961). A shift from an upright to a horizontal sleeping position occurred in the symmetrical ancestors of the flatfish; sleeping on either side is done in some of the present-day symmetrical acanthopterygians, such as triggerfish and wrasses. If this sleeping position were maintained as a resting or hiding position after the animal awoke, a shift of the eye from the blind towards the upper-most side would be an advantageous modification. The shift of the eye on the blind side to the margin of the head would enable the fish to scan the waters above it with binocular vision (Wahlert 1965: 290).

But von Wahlert's suggestion hardly solves – hardly addresses – the questionable adaptive value of the initial stages of eye migration, and that Goldschmidt (and Mivart) tried to circumvent by invoking an all-at-once transformation. On the other hand, starting with the deeper ancestral state of a vertical lifestyle, as von Wahlert does, followed by the evolution of horizontal *resting*, does seem a promising solution to a different puzzle, namely how flatfishes acquired a horizontal *lifestyle* in small steps each of which was selectively favoured. That is, they spent more and more waking time in what was previously just a resting posture, taking more and more advantage of that less conspicuous and motionless position to avoid predators and surprise prey.

And this has the elements of a worthwhile narrative. The acquisition of horizontal resting was hardly guaranteed. Indeed, von Wahlert offers no suggestion as to how it came about. His narrative discloses what was not foreseeable, a basic function of a worthwhile narrative. Moreover, once disclosed, the acquisition of horizontal resting serves as a counterfactual difference-maker in his narrative; it is consequential. Consider the counterfactual alternative: that horizontal resting was not acquired prior to acquisition of a horizontal lifestyle. It is not at all clear how the small steps from a vertical lifestyle directly to a horizontal lifestyle could be advantageous. What could be the advantage of tilting just slightly from vertical to horizontal?

As for the gradual transformation from a vertical lifestyle to horizontal resting, well, any suggestions?[10]

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[10] I am very grateful for the opportunity to participate in the Narrative Science Project. Thank you Mary, Kim and Dominic, and thanks to fellow participants for their feedback and wealth of perspectives. I'm very lucky to join you in this volume. I was also lucky to contribute to the 2017 special issue of *Studies in History and Philosophy of Science, Part A*, devoted to scientific narratives, and edited by Mary and Norton Wise. *Narrative Science* book: This project has received funding from the European Research Council under the European Union's Horizon

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