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The proper role of history in evolutionary explanations

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Abstract

Evolutionary explanations are not only common in the
biological sciences, but also widespread outside biology. But an account of how evolutionary explanations
perform their explanatory work is still lacking. This
paper develops such an account. I argue that available accounts of explanations in evolutionary science
miss important parts of the role of history in evolutionary explanations. I argue that the historical part of
evolutionary science should be taken as having genuine explanatory force, and that it provides how-possibly
explanations *sensu* Dray. I propose an account of evolutionary explanations as *comparative-composite explanations* consisting of two distinct kinds of explanations, one
processual and one historical, that are connected via the
explanandum's evolvability to show how the explanandum is the product of its evolutionary past. The account
is both a reconstruction of how evolutionary explanations in biology work and a guideline specifying what
kind of explanations evolutionary research programs
should develop.

1 | INTRODUCTION

How do evolutionary explanations explain? Notwithstanding the overwhelming explanatory successes of evolutionary biology and the increasing use of evolutionary explanations in the social and human sciences, this question remains open and a general account of evolutionary explanations as a distinct mode of scientific explanation is lacking. There are several reasons for this.

For one, it is insufficiently clear what exactly we are talking about when discussing evolutionary explanations. While sometimes 'evolutionary explanation' is used to simply mean "the set of explanatory styles" that can be found in evolutionary biology (Huneman, 2013: 714), this set is much too diverse for a general account to be possible. Philosophers of biology have distinguished a plurality of modes of explanation used in evolutionary biology, including selection explanations (McLoone, 2013), phylogenetic inertia explanations (Griffiths, 1996; Orzack & Sober, 2001), lineage explanations (Brown, 2014; Calcott, 2009), homology explanations (Ereshefsky, 2012), evolvability-based explanations (Brown, 2014), part-whole explanations (Winther, 2011), topological explanations (Huneman, 2010; 2018), and more. According to Huneman, "biology and especially evolutionary biology and ecology are characterized by a pluralism regarding explanation, in the sense that distinct explanatory modes coexist in those fields" (2018: 116). But which of these modes of explanation should count as *evolutionary* explanation? Are some (or all) of them different *kinds* of evolutionary explanation – does the category of evolutionary explanations subdivide into different kinds? Or are they best seen as *components* of evolutionary explanations, or as *partial* evolutionary explanations? Topological explanations and part-whole explanations, for example, are important parts of evolutionary science, but do not constitute different kinds of evolutionary explanation, as they do not rest on evolutionary theory and also occur outside the evolutionary sciences. But they add non-evolutionary explanatory elements to evolutionary explanations and as such can still be crucial components of full-fledged evolutionary explanations.

An additional problem is due to the heavy emphasis that is usually placed on natural selection in evolutionary explanation. While biologists generally recognize that evolutionary explanations must encompass a historical narrative about the evolutionary past of a trait as well as a description of how the selection process occurred, often the historical part is seen as merely providing the context within which the process played out. The actual explanatory work is done by the processual part and the general principles of selection theory, it is thought, while the historical part plays a role similar to that of the initial conditions in Deductive-Nomological explanations. Such a – I believe, overly narrow – view equates evolutionary explanations with selection explanations. It can, for example, be found with Rosenberg (2001; 2006; 2007), who argued that the only laws of biology are the laws of natural selection and that these do all the explanatory work.[1] As he wrote:

> "Biology is indeed a historical discipline. But the main principles of Darwin's theory […] are the only (*ceteris paribus*) laws of biology. And it is the application of these laws to initial conditions that generates the functional kinds which make the rest of biology implicitly historical […] [Biology's] explanations are 'historically' limited by the initial distribution of matter on the earth, and the levels of organization into which it has assembled itself." (Rosenberg, 2001: 758)

And, indeed, in publications on evolutionary research the historical part is often limited to a brief description of relevant circumstances at some point in evolutionary history against the background of which traits and other biological explananda are then explained by specifying how the explanandum provided a selective advantage under the specified circumstances.

But approaches that emphasize selection as the principal or even only explanatory factor face several issues. One is the unresolved question *how* selection explains, which arises from the ongoing debate on the nature of selection, that is, the question whether selection is best conceived of as a force (Hitchcock & Velasco, 2014; Sober, 1984), a mechanism (Barros, 2008; Skipper & Millstein, 2005), a statistical outcome of lower-level processes (Walsh, 2000; Walsh et al., 2002; 2017), or something else. Different answers to this question yield different accounts of how selection explains evolutionary phenomena. Another, related, question is *what* exactly selection explains, which is a question that involves at least two different debates. The first is the debate on the innovative potential of natural selection. This debate revolves around the question whether natural selection actually explains the emergence of novel traits or only their persistence and fixation in lineages once they have arrived on the scene (i.e., whether selection explains the "arrival of the fittest" or merely the "survival of the fittest" – see: De Vries, 1904: 825-826; Fontana & Buss, 1994; McLaughlin, 2011; Reydon, 2011). The second is the ongoing debate on the "Negative View" of selection (Birch, 2012; McLoone, 2013; Pust, 2001; Stegmann, 2010), which focuses on the question whether natural selection explains the traits of individual organisms, or only trait distributions in populations.

Moreover, selection is neither a necessary nor a sufficient ingredient of evolutionary explanations. While selection is a central aspect of biological evolution, evolution without selection commonly occurs too (most prominently through genetic drift). Conversely, not every selection process is an evolutionary process – consider mere filtering processes without the production of new variation. Biological evolution encompasses a much more diverse and complex set of processes and causal factors besides straightforward selection – including mutation, drift, migration, geographical isolation, developmental canalization, developmental constraints, phylogenetic inertia, epigenetic inheritance, etc. –, and evolutionary explanations should adequately represent this processual diversity and complexity. Simply highlighting selection as *the* explanatory core of evolutionary explanations is insufficient as an account of how actual evolutionary explanations explain.

In addition, it should be noted that *even if* selection could be taken as the principal explanatory factor in evolutionary explanations, there is a plurality of perspectives on selection processes that yield distinct selection explanations. Natural selection can be seen from Dawkins' "gene's eye" view, Darwin's organism-level perspective, Mayr's population-level perspective and Gould's species- or lineage-level perspective. Accordingly, Sterelny and Kitcher (1988; Sterelny, 1996) argued for an "ecumenical conception of explanation" (Sterelny, 1996: 194) in evolutionary biology. According to these authors, the same evolutionary phenomenon can be explained by taking various perspectives on the selection process, with macroevolutionary explanations latching onto higher levels of organization and microevolutionary explanations latching onto lower levels of organization. All constitute complete, mutually irreducible, and complementary explanations, each providing different information that is only accessible from its particular perspective: "[d]istinct explanations of the same event can both be important, for they can convey distinct breeds of modal information" (1996: 195). A complete evolutionary account of the phenomenon would thus encompass a set of selection explanations "seeing" selection from different perspectives. This entails that *the* evolutionary explanation of a biological phenomenon does not exist. There are multiple such explanations, each by itself a complete evolutionary explanation of the phenomenon and taken together constituting a multi-perspectival evolutionary explanation.[2]

When it comes to explanation, then, evolutionary science is deeply pluralistic. This makes it impossible to devise a fine-grained, overarching account of how evolutionary explanations explain. And it suggests that there is no point to talking about evolutionary explanations as a separate category of scientific explanation: evolutionary science seems to invoke a plurality of modes

of explanation within which no unity is to be found. In the present paper, I want to counter this appearance by showing that at a more coarse-grained level the questions what makes an explanation into an *evolutionary* explanation, how evolutionary explanations are structured, and how they explain, might still be answerable. Without aiming for a complete answer I will address these questions by clarifying the coarse-grained general structure of evolutionary explanations to show how their explanatory machinery works and what fundamentally distinguishes them from other kinds of explanations.

I will proceed as follows. Before entering into my argument, Section 2 introduces the notion of comparative-composite explanation and highlights the main novel elements of the account presented in this paper. In Section 3, I will show how explanatory pluralism leads to two interconnected explanatory risks for evolutionary research. Section 4 shows how evolutionary biologists deal with those risks by invoking history. Sections 5–6 develop what I call the *comparative-composite account of evolutionary explanations* by showing that evolutionary history performs its own separate, genuinely explanatory role (as opposed to merely providing background information for processual explanations). Section 7 shows how the processual and historical parts of evolutionary explanations are connected via the concept of evolvability. Section 8 concludes by explicating the proper role of history in evolutionary explanations.

2 | COMPARATIVE-COMPOSITE EXPLANATION

I argue that evolutionary explanations should be conceived of as *comparative-composite explanations* consisting of two kinds of explanations, one a processual and regularity-based explanation, the other a historical how-possibly explanation, that are connected via the explanandum's evolvability to show how the explanandum is the product of its evolutionary past. The two explanations are explanatorily independent (Potochnik, 2010) in the sense that each is "satisfactory despite black-boxing details which the other emphasizes" (Currie, 2021: 18). That is, as part of an evolutionary explanation the historical how-possibly explanation fully explains *its* explanandum while black-boxing details about the evolutionary process, the processual explanation fully explains *its* explanandum while black-boxing details about history, and both joined together provide a complete evolutionary explanation of the trait or trait distribution under examination. Before proceeding, let me clarify some terminology.

What I call a *processual explanation* is an explanation that explains by showing how a process produces an explanandum. The traditional modes of scientific explanation that are widely discussed in the literature, such as Deductive-Nomological explanations or mechanistic explanations, are processual explanations: they specify the primary aspects of processes (the laws that govern processes of a particular kind, or the way in which parts of a mechanism interact to produce an effect). Adaptive or selection explanations, as well as explanations invoking genetic drift, are processual explanations in this sense: they refer to the regularities governing evolutionary processes. Processual explanations are what the natural sciences typically seek.

How-possibly explanations – by which I mean the specific type of historical explanations introduced by Dray (1957; 1964; 1968) – are much less in view in the natural sciences than processual explanations. Confusingly, at least two very different modes of explanation besides Dray's how-possibly explanations have also come to be called 'how-possibly explanation' (Pearson, 2018). Brandon (1990), Resnik (1991); Reydon, 2012 and Griffiths (1994: 222; 1996: 514) use 'how-possibly explanation' to mean *possible explanations* in the sense of ordinary Deductive-Nomological explanations of which the initial conditions are merely speculative, such that the explanation remains

incomplete and merely hypothetical. That is, as long as the initial conditions have not been established, the explanation remains merely possible. Griffiths (1994: 222) even equated how-possibly explanations to Gould's "just-so stories."

Recently, Rohwer and Rice (2013), Reutlinger et al. (2018) and Sullivan (in press) have introduced yet another meaning of 'how-possibly explanation'. What these authors mean by how-possibly explanations are models that show that a particular phenomenon is possible *in principle* by specifying possible processes that can produce it, without saying anything about the actual process that occurred or the actual historical state of affairs at the outset of the process. Accordingly, "[t]he explanans of how-possibly explanation refer to *merely possible explanatory factors* (for instance, to possible causes and mechanisms bringing about the explanandum phenomenon [. . .])" (Reutlinger et al., 2018: 1085; emphasis added). Or: "a how-possibly explanation simply *highlights a possibility concerning the causes or dependencies of some phenomenon*; it falls short of explaining how the target phenomena *actually* is caused or the actual dependencies concerning the phenomenon" (Sullivan, in press: 20; emphasis added). Neither of these two usages of the term 'how-possibly explanation' correspond to how-possibly explanations *sensu* Dray, which show the possibility of the phenomenon by highlighting *actual* historical factors that obtained at a particular time *t* and allowed the trajectory that eventually led to a state of affairs at a later time *t'* to *actually* occur.

Dray's how-possibly explanations tell the actual historical story to show how an improbable event was possible, whereas Brandon's and Resnik's how-possibly explanations only speculate about history, and the (non-historical, model-based) how-possibly explanations discussed in the recent literature on models tell only possible stories. Both kinds are very different kinds of explanations from Dray's how-possibly explanations. I emphasize again that I only use the term 'how-possibly explanation' in Dray's sense (see Section 6 for more details).

The account proposed here is a reconstruction of the general structure of evolutionary explanations as a *genre* of scientific explanation found in evolutionary biology. By 'genre of scientific explanation' I mean an overarching mode of explanation of which concrete instances can differ considerably in the details while all sharing the same way of reasoning. I call evolutionary explanation a 'genre of explanation', because on the account presented here evolutionary explanations are composite explanations that contain different kinds of scientific explanations as their component parts – they are explanations made of other kinds of explanations joined together (a how-possibly explanation in the specific sense of Dray's work plus a processual explanation, which may be a law-based explanation, a mechanistic explanation, or some other mode of explanation that highlights the workings of a process). My claim is that all evolutionary explanations share this global structure, which explicates what gives them their specific kind of explanatory force, while the evolutionary explanations used in different contexts of research will diverge widely with respect to the ingredients contained in the processual and the historical parts. As such, the account unifies the category of evolutionary explanations while at the same time allowing for considerable explanatory pluralism in the evolutionary sciences.

Parts of the account of evolutionary explanations presented here can be found in the literature and are often – usually implicitly – endorsed by practicing biologists (in particular those working in the area of evo-devo). But I believe that the complete picture is not widely seen. One novel contribution of this paper consists in making the complete picture explicit (by joining the various parts into an account of the general structure of evolutionary explanations). Moreover, I want to defend the following specific claims, which together constitute a novel, detailed account of evolutionary explanations and of the proper role of history in them:

- The historical parts of complete evolutionary explanations always include how-possibly explanations in the specific sense introduced by Dray.
- The historical parts of evolutionary explanations *individuate traits as explananda*. They show a trait can be singled out as a distinct product of evolution on the basis of comparisons to traits occurring in closely related lineages.
- In so doing, they *explain the possibility of the evolutionary trajectory* that was taken by specifying the ancestral trait state from which the trajectory started (and that would have led to a different trajectory if the ancestral state had been different) as well as aspects of the ancestral environment that made the trajectory possible.
- The two kinds of explanations of which evolutionary explanations consist, how-possibly explanations and processual explanations, are connected into evolutionary explanations by the notion of evolvability. The how-possibly explanation explains how the evolutionary trajectory *was possible* (by specifying how organismal properties, population structure and environmental factors determine the evolvability of the explanandum), while the processual explanation explains how the trajectory *actually occurred* (by specifying aspects of the evolutionary process, such as selection and drift).

While developing this account, I also present a novel critique of some aspects of Rosenberg's, and Orzack and Sober's views of the role of history in evolutionary explanations.

The account presented here takes history and processes equally seriously as performing explanatory work. But because of the explanatory role of history and the fact that often historical information is insufficiently available, complete evolutionary explanations will be hard to achieve in practice. Still, the account presented here does not only provide philosophical understanding of how evolutionary explanations explain, but can also serve as a guideline that specifies which kinds of explanatory components researchers in the evolutionary sciences should be looking for to formulate complete evolutionary explanations.

3 | EXPLANATORY RISKS

The problems caused by explanatory pluralism can be illustrated by Gould and Lewontin's (1979) famous critique of adaptationism. Gould and Lewontin highlighted two explanatory risks associated with adaptationist thinking, entailed by the two central aspects of adaptationist thinking, namely "breaking an organism into unitary 'traits' and proposing an adaptive story for each considered separately" (Gould & Lewontin, 1979: 581).

The first explanatory risk on the adaptationist approach is that of *misidentifying the explanandum* – the risk that putative traits are carved out as explananda while not being suitable as focal phenomena of the kind of explanation that is envisaged. Organisms do not come pre-divided into traits for which explanations can be sought, but researchers must individuate traits as explananda for their specific explanatory projects. Multiple ways of decomposing an organism into traits are always available (Love, 2008: 69-71), and traits are individuated in the specific contexts of investigative projects which involve choices for particular modes of explanation. How the explanandum is fixed thus is in part guided by which modes of explanation the investigators are interested in. Gould and Lewontin (1979: 585) did not explicitly address the question what traits are, but provided the human chin as an example of incorrect trait individuation: a chin is not a separate trait when seeking an adaptationist explanation, but is better explained as an aspect of a different explanandum (skull allometry).

The second risk is that of *misidentifying the explanans* – the risk of remaining stuck on an incorrect mode of explanation once the explanandum has been fixed. Gould and Lewontin noted that it is just a little too easy to come up with adaptationist stories about organismal traits, such that there might be too little incentive to search for explanations of a different kind. As they put it:

> "the rejection of one adaptive story usually leads to its replacement by another, rather than to a suspicion that a different kind of explanation might be required. Since the range of adaptive stories is as wide as our minds are fertile, new stories can always be postulated. [...] [T]he criteria for acceptance of a story are so loose that many pass without proper confirmation. Often, evolutionists use *consistency* with natural selection as the sole criterion and consider their work done when they concoct a plausible story. But plausible stories can always be told. The key to historical research lies in devising criteria to identify proper explanations among the substantial set of plausible pathways to any modern result." (Gould & Lewontin, 1979: 587-588)

The authors' point is that adaptationist explanations are difficult to test: usually, numerous evolutionary pathways to a trait are consistent with evolutionary theory (some involving selection on the trait in question, others not) and information about evolutionary history is required to adjudicate between theoretically plausible pathways. But often sufficiently detailed knowledge about past circumstances is unavailable, such that the evidence severely underdetermines the choice between potential explanations. As Orzack and Forber (2017: Sec. 3.2), observed, "[i]n principle, rival hypotheses make different commitments about the nature of evolutionary history, but in practice these hypotheses are empirically indistinguishable given the available evidence."

Griffiths (1996: 512-514, 518; also 1994: 221-222) highlighted the same problems as Gould and Lewontin, but approached them from the adaptive problems researchers hypothesize ancestral populations to have faced, rather than from the traits that are supposed to have solved these problems (which was Gould and Lewontin's perspective). According to Griffiths, adaptive thinking faces the problem of complacency with respect to identifying the adaptive problem that a trait is supposed to have solved, and the problem that a particular adaptive problem is solved in different ways in different lineages. The former amounts to what I have called misidentifying the explanans. Griffiths pointed out that the presence of a trait often is compatible with an otherwise unsupported hypothesis about the nature of the adaptive problem the trait is supposed to solve. Alternative hypotheses about different adaptive problems, as well as non-adaptive scenarios regarding the origin of the trait, thus are easily ignored, because the trait's presence makes sense in light of the adaptive problem that has been hypothesized to have existed. At base, this boils down to ignoring alternative explanantia because the trait makes sense in light of a favored explanans. The latter problem highlighted by Griffiths corresponds to misidentifying the explanandum. Griffiths pointed out that often different traits in different lineages have arisen in response to the same adaptive problem. *Starting from a particular adaptive problem*, multiple solutions thus are possible, which means that it is unclear whether a trait that is in focus (such as the human chin) actually arose in response to the adaptive problem under consideration. Researchers can start by assuming an adaptive problem and then identify a trait that solves it, or by individuating a trait and then hypothesizing about an adaptive problem that the trait allegedly solves. Either way, there is the same risk of misidentifying the explanandum for their project to investigate. Griffiths (1996: 519) argues that a comparative perspective is crucial to address these two problems – something I will also argue in the following section.

Griffiths, and Gould and Lewontin, emphasize the importance of history, but hold diverging views of its role. What Griffiths (1996) called the "historical turn in the study of adaptation" is

> "the realization that adaptive generalizations [...] cannot explain form except *in conjunction with* a rich set of historical initial conditions. [...] Selection processes are historical because the relative fitness of characters is a function of the historical conditions in which selection takes place and of the complete range of alternative characters present (which is a function of past history)" (Griffiths, 1996: 515; emphasis added).

This historical turn thus consists in the acknowledgement that adaptive generalizations are unable to explain traits without the addition of historical conditions. Griffiths (1994: 222) suggested that "adaptive explanation must become adaptive-historical explanation," with historical information transforming possible processual explanations into actual explanations. History does not perform explanatory work of its own, though, and in the end adaptive-historical explanations *just are* adaptive explanations where the explanatory work is done by the generalizations describing how the evolutionary process took place under the specified initial conditions (as on Rosenberg's view cited above).

Gould and Lewontin, in contrast, were primarily concerned with the explanatory role of historical constraints on organismal development: contrasting selection and history, they argued that historical constraints often adequately explain a trait *rather than* natural selection. But explanation by constraints alone is not a good alternative to explanation by selection or another evolutionary process: even if constraints explain a trait, only invoking constraints seems insufficient and the historical explanation still needs to be complemented by an account of the actual process(es) that brought about the trait.[3] Even the human chin cannot be explained by only invoking constraints on skull growth (as Gould and Lewontin suggested) – an adequate explanation should also explicate how growth processes and the evolution of skull shapes *actually* occurred (e.g., Holton et al., 2015). In contrast to both the historical turn that Griffiths highlighted (with history providing crucial background information, but explanatory force located with the generalizations that describe evolutionary processes) and Gould and Lewontin's view (who suggest that historical constraints can explain traits without taking recourse to process generalizations), I suggest in what follows that explanatory force should be located with both kinds of factors.

This need for a processual part in the explanation exacerbates the misidentifying-the-explanans problem, because the process-focused part of evolutionary biology involves much more than just selection and can refer to a multitude of regularities that pertain to how evolutionary processes generally occur. Darwin's principle of natural selection (or "Darwin's schema" – Lewontin, 1970) and the principle of genetic drift are the most prominent such evolutionary regularities, but not the only ones. Darwin himself asserted that he was "convinced that natural selection has been the main but not exclusive means of modification" (Darwin, 1859: 6; Gould & Lewontin, 1979: 589) and ever since there has been a debate on the question how much exactly natural selection explains (Sober & Orzack, 2003: 424-425; Love, 2008).

In Wallace's and Weismann's late nineteenth- and early twentieth-century Neo-Darwinism natural selection occupied the central place as *the* cause of organismal form and adaptation. In the Modern Synthesis of the mid-twentieth century, selection still occupies a central position, but the Modern Synthesis is clearly less panselectionist than Neo-Darwinism. And the centrality of selection also lies at the heart of the recent debate on a possible Extended Synthesis. Proponents of an Extended Synthesis argue that the standard Modern Synthesis view of evolution rests on an incom-

plete collection of explanatory factors, focusing too much on genes as the loci of causation. On their view, important causal factors in the evolutionary process (most importantly pertaining to organismal development, niche construction and non-genetic systems of inheritance) have been overlooked and should be added to the explanatory arsenal of evolutionary theory (e.g., Baedke et al., 2020). Evolutionary biologists thus can invoke a multitude of processes to explain evolutionary phenomena, and the phenomena themselves underdetermine which process is applicable.

Note that the two explanatory risks are interconnected, because they ultimately both root in the explanatory pluralism that is characteristic of evolutionary biology. An explanation might be wrong because the explanandum is not well-chosen for the particular explanatory project in which it is considered, or because it invokes the wrong kind of explans even when the explanandum is well-chosen for the approach. While Gould and Lewontin specifically took aim at overly adaptationist thinking in biology, I suggest that the explanatory risks they highlighted apply more widely to all areas of investigation in which complex phenomena are investigated from an evolutionary perspective, both within the biological sciences and beyond. Let me explain.

Both explanatory risks result from the fact that organisms do not come pre-carved as bundles of traits and different explanatory perspectives often require different carvings. This is not a unique situation for living organisms, though. Hardly *any* entities we find in the world (except perhaps elementary particles that are defined by their essential properties, and artifacts of which all properties have been specified in advance by their designers in detailed design plans) come as straightforward bundles of pre-individuated traits or properties. Traits and properties are individuated by us, and different perspectives often yield different ways of individuating traits and properties. And explanatory pluralism is not unique for evolutionary biology either, but occurs widely in the sciences (Mantzavinos, 2016). The highlighted explanatory risks should thus generally be expected when investigating complex, functionally organized entities.

Since trait individuation depends in part on the explanatory perspective, this yields a circle that is difficult to break: *For complex entities, it generally is not possible to individuate traits in need of separate explanations independently of hypotheses about the details of the explanation. A trait is only a trait in relation to an explanatory project. However, it generally is not possible to devise explanations of the traits of complex entities independently of hypotheses about what their traits are*. Because of this, evolutionary explanations generally are risky. However, evolutionary biology has a way to tackle this problem.

4 | COMPARATIVE BIOLOGY

The key to tackling these explanatory risks is acknowledging something that biologists and philosophers of biology have long recognized: that evolutionary biology is a thoroughly *comparative* science (Currie, 2021; Griffiths, 1994; 1996; Wagner, 2014; 2016).

For one, trait individuation is comparative. "Carving up" organisms into traits proceeds by comparing organisms of related species and identifying similar features (morphological structures, DNA sequences) in members of different species. Accordingly, the notion of homology underwrites trait individuation (Wagner, 1996; 2014: 51-54; 2016: 4-5; Griffiths, 1996: 528; 2006; 2007; Love, 2008; Ereshefsky, 2009; 2012). But explanations, too, are comparative. For instance, classical genetics does not explain phenotypes through genotypes, but rather phenotype differences through genotype differences (Waters, 1994). Rather than explaining a fruit fly's white eyes by its having a particular allele at a particular locus (*white*) of its genome, geneticists explain the difference of the fly's eye color from the wild type (red eyes) by its having a mutation at the *white*

locus (in contrast to the wild type allele occupying that locus). Both the explanandum (eye color) and the explanans (genetic underpinning) are comparative – the explanation explains why a trait differs from an expected default state.

The same holds for explanations in evolutionary biology. Evolutionary biology does not explain traits and trait distributions *tout court*, but rather evolutionary novelties and changes in trait distributions. Consider again the human chin. Attempts to formulate adaptationist explanations of the human chin considered by itself go awry, because stand-alone adaptationist stories are difficult to test. But using comparisons to closely related species and early members of our own species helps. Humans are the only animals with chins, and not all early members of *H. sapiens* seem to have had chins (Holton et al., 2015; Schwartz & Tattersall, 2000; Yong, 2016). Comparison to our closest relatives thus tells us that the ancestral state was "no chin," and "chin" is an evolutionary novelty. It would be very unlikely – but not impossible – to find a trait state in only one species and no closely related species if it were the ancestral state.

This provides us with a useful perspective on Gould and Lewontin's complaint that adaptationist stories about chins were all too easy to come up with. You can try it for yourself: it is easy to speculate how a chin could be an adaptation for mate attraction, for impressing competitors for mates, for being able to chew tougher materials (a chin deflects bending stress on the jaws during mastication, making chewing raw meat easier, providing early humans with the proteins needed for brain development, leading to present-day intellectual capacities), for battling competitors and enemies (a pronounced chin might serve to deflect punches received on the lower part of the face and make jaws less breakable), or for something else. All these stories about the selective advantage that *might* have been involved in evolution from the "no chin" to the "chin" state involve the same process (adaptation by natural selection in response to specific selection pressures), but with different details regarding the selective factors in play. The number of possible stories can be reduced by comparison with our chin-less relatives, which sheds doubt on the speculations that the chin might be an adaptation for meat eating or for deflecting punches. In any of those cases, chins should be found with early ancestors who also ate meat or regularly got into fights, and should therefore also be found with at least some of our contemporary relatives. But this is not the case: chin-less chimpanzees and bonobos eat meat and meat eating evolved long before the origin of *Homo sapiens* (there is fossil evidence for meat eating in some species of *Paranthropus* and *Australopithecus* – Pobiner, 2013). Neanderthals primarily ate meat (Jaouen et al, 2019), but did not have chins.[4] And probably all ancestors of *Homo sapiens*, as well our contemporary non-human relatives, regularly got into fights, yet none have chins. This does not mean that chins did not result from adaptive selection at all, but it does cull a few of the scenarios from the many possible ones.

Understanding the explanandum as not being the chin as such, but the *transition* from "no chin" to "chin" in the lineage of *Homo sapiens*, enables the testing of adaptive hypotheses (Griffiths, 1994: 222-224; 1996: 521-524; Currie, 2021: 19). Adaptive explanations concern the direction of change in a lineage (Orzack & Sober, 2001: 50), and to construct adaptationist explanations one needs information about the polarity of the trait under consideration – "information about what has evolved from what" (Brandon, 1990: 171; see also Griffiths, 1996: 522-524; Wagner, 2016: 5-6). This does not only hold for adaptive explanations: *any* explanation of an evolutionary novelty concerns the direction of change in a lineage.

Orzack and Sober (2001; see also Sober & Orzack, 2003) provided a theoretical foundation for the claim that adaptationist explanations are only testable in combination with suitable background assumptions about the actual evolutionary history of the lineage. Such assumptions, they argued, can be obtained from the principle of common descent. The principles of natural selection

and of common descent – the two principal components of the Darwinian theory of evolution – are logically independent but evidentially connected, they argued. Because of convergent evolution, highly adaptive traits tend to provide little information about ancestral relations, such that the stronger the evidence that a trait is produced by selection the weaker the evidence for common descent (Sober & Orzack, 2003: 427-428). Conversely, if several species have a recent common ancestor, their separate evolution started out from the same ancestral state and the levels of heritability of the trait will be very similar in all species: "[t]he effect of common ancestry is that lineages begin evolving with the same heritability, just as they begin evolving with the same trait value" (Sober & Orzack, 2003: 433-434). Thus, in closely related species, the material basis of evolution and the various aspects of the evolutionary process internal to the evolving systems are very similar, allowing them to be compared with respect to different external influences on the evolutionary process.[5] If extant species are very closely related, one can even serve as a proxy for the other's ancestor (Orzack & Sober, 2001: 54). For the human chin, the absence of chins in other primates suggests that "no chin" is the ancestral state, providing a common background against which the strength of natural selection can be assessed. A hypothesis of common ancestry thus provides a necessary (though not generally sufficient) background assumption that renders the hypothesis of natural selection testable.

Consider a recent study of the evolutionary origins of paedomorphic facial expressions in dogs. The authors

> "tested whether humans (when adopting dogs from a shelter) actively select for dogs which appear more juvenile in the face as a result of facial muscle contraction [...] using real world shelter dog adoption speed as a proxy for human selection over evolutionary time." (Waller et al., 2013: 2)

From empirical data about differential selection of dogs from shelters the authors concluded

> "that domestic dogs who exhibit paedomorphic characteristics are preferentially and actively selected by humans as pets from rehoming shelters. This therefore supports the hypothesis that paedomorphic characteristics in domestic dogs arose as a result of indirect selection by humans rather than only being a by-product of selection against aggression." (Waller et al., 2013: 5)

The authors inferred a possible selection explanation for canine paedomorphic facial expressions from observations of present-day selection processes and historical knowledge that dogs were domesticated by early humans. They admitted that such inferences from observations of current selection to claims about past selection are problematic, but nevertheless assumed that these are warranted.[6]

The authors supported this assumption by invoking comparisons between species. In later work, researchers from the same collaboration compared eyebrow movements and facial muscle anatomy between contemporary dogs and wolves, showing that dogs exhibit eyebrow movements more frequently and more intensely than wolves, which generally lack facial muscle structures necessary for exhibiting strong paedomorphic facial expressions (Kaminski et al., 2019). These comparisons between two closely related species, *Canis lupus* and *Canis familiaris*, suggested that facial paedomorphosis is the descendant state (if it had been ancestral, similar muscle structures should have been found in wolves too, either in functional or in vestigial form). This finding thus determined the explanandum for the proposed selection explanation (the change from

"no paedomorphosis" to "paedomorphosis") and in this way made the possible selection explanation more concrete by specifying which evolutionary trajectories would be compatible with the explanandum and which would not. This rendered the proposed selection explanation testable by invoking knowledge about the actual evolutionary history of dogs from wolves.

The picture that I have sketched so far shows that knowledge about evolutionary history constitutes a crucial part of evolutionary explanations in at least two roles: adding information about initial conditions and constraints, and making hypothesized adaptive explanations testable. This picture is not new, but in what follows I will argue that it is incomplete. In this picture history does not perform explanatory work of its own – it merely makes non-historical explanations (pertaining to the *process* that caused a trait's presence) possible. The explanatory force is still located entirely with the processual part of the explanation. I will now show that this picture it misses the important fact that the historical side, too, performs crucial, genuine explanatory work of its own.

5 | WHAT HISTORY EXPLAINS: POSSIBLE PATHWAYS TO INNOVATION

Conceiving of the historical part of evolutionary biology as having genuine explanatory force is in line with Darwin's views. Darwin (1859: 159) referred to community of descent as a *vera causa*, a real cause of biological phenomena, and specified that "propinquity of descent [is] the only known cause of the similarity of organic beings" (1859: 413).[7] In the *Origin* Darwin highlighted the explanatory force of the principle of common descent: "large bodies of facts, otherwise inexplicable, can be explained by the theory of descent" (1859: 188), "[o]n my theory, unity of type is explained by unity of descent" (1859: 206), "extinct and living species [...] all fall into one grand natural system; and this fact is at once explained on the principle of descent" (1859: 329), and: "on the theory of descent with modification, the main facts with respect to the mutual affinities of the extinct forms of life to each other and to living forms, seem to me explained in a satisfactory manner. And they are wholly inexplicable on any other view." (1859: 333).[8] The similarities in question are homologues, connecting trait individuation to the underlying explanations of trait presence.

A comparison of Darwin's view to Orzack and Sober's view can illustrate why Darwin was right that history explains. Orzack and Sober saw common descent as not exerting any explanatory force itself but merely enabling the testing of adaptive explanations. But this cannot be the complete story, because the historical comparison determines *what there is to explain* in the first place. Historical information does not only identify an evolutionary trajectory as the explanandum for which a processual explanation is sought, but also shows why this trajectory can be explained by the particular processual explanation that is under consideration. The historical comparison between dogs and wolves, discussed above, identifies the trajectory from "no paedomorphosis" to "paedomorphosis" as an explanandum, but also supports a possible selection explanation for this trajectory. Historical explanations thus explain how the various descendant trait states under consideration *could possibly have evolved* from an ancestral state.

The idea is that before describing the concrete processes that occurred in an actual evolutionary trajectory, researchers must first establish that the occurrence of this process (leading from ancestral to descendant state) was possible at the time of the ancestral state. Because the processes in question transform ancestral trait states into descendant states (or retain the ancestral state by stabilizing selection), establishing the possibility of the processes starts with determining what the ancestral state could have been and subsequently establishing the possibility of evolutionary trajectories leading from that ancestral state to descendant states. As Wagner put it, it "requires first

to learn as much as possible about the structure and function of the ancestral state from which the derived state (the explanandum) evolved […] The purpose is to understand the starting point and the mechanistic possibilities that existed before the transformation ensued." (2016: 5).[9] This fixes the explanandum for the processual explanation (*not* the descendant state, but the change from ancestral to descendant state), which then can be invoked to show how the change process actually played out.

The need for establishing the possibility of the trajectory before devising a processual explanation stems from several aspects of evolution. First, evolutionary transitions considered outside any historical context generally have very low probability, making it necessary to show that given the right circumstances a particular transition's probability is higher than would be expected from considering the transition independently of any circumstances. Moreover, evolution is a process of "tinkering" (Jacob, 1977) – a process of innovation by modifying existing organismal structures, such that at any time the scope of possible future innovations is constrained by what is available at that time. Gould and Lewontin emphasized that organisms are "so constrained by phyletic heritage, pathways of development and general architecture that the constraints become more interesting and more important […] than the selective force" (1979: 581). In addition, future innovations are constrained by stabilizing selection on available structures that prevents them from diverging too far from their current state (Charlesworth et al., 1982; Griffiths, 1996). But existing structures do not only constrain innovation – they also *make innovation possible* in the first place by providing the material basis for evolution to tinker with, thus opening up a space of possible pathways. From any given structure a set of pathways for building new structures is possible while others are closed, as certain parts of the space of possible structures cannot be reached by starting from what is available. Starting out from another structure opens up and closes different sets of pathways. Gould and Lewontin (1979: 593) pointed out that closely related species and subspecies often evolve different adaptations to the same environment when there are multiple adaptive "peaks," with differences due to differences in organismal structures the various populations started out with.

Biologists and philosophers of biology have long recognized the importance of organismal structures and developmental pathways in constraining as well as opening future evolutionary trajectories. Consider for example Waddington's (1942; 1957; 1959) work on developmental canalization and Wimsatt's (1986; 2001; 2007: Chapter 7; 2013; 2015; Schank & Wimsatt, 1987; 2000) work on generative entrenchment. Generatively entrenched structures are both strongly conserved in evolution and set paths for the development of novel structures: "deeply entrenched features have both of these characteristics: species-typical evolutionary conservatism, and a generative role in producing characteristics of individuals" (Wimsatt, 2013: 320).[10] This capability of developmental factors to affect evolutionary pathways is widely recognized in the tradition of evo-devo (e.g., Wagner, 2016) and is becoming commonly accepted in evolutionary biology more broadly. Ancestral trait states and organismal structures thus explain an actual pathway from an ancestral state to a novel state by showing how it was made *possible* by the material that was available for evolutionary processes to work with. Processual explanations add to this by showing how the evolutionary process actually played out to realize this pathway.

Evolutionary history thus has genuine explanatory force of its own. It complements processual explanations by explaining how the processes described by the latter were possible in the first place. Having established this, I will now argue that the way in which such historical explanations explain is the way in which *how-possibly explanations* in historical research explain.

6 | HOW HISTORY EXPLAINS: HOW-POSSIBLY EXPLANATIONS

The notion of how-possibly explanations was introduced by Dray (1957: 156-169; 1964: 18ff.; 1968) in contrast to the (at the time) dominant covering law account of scientific explanation. For reasons of space, I can only give a brief account of how-possibly explanations – for more extensive discussions, see Reydon (2012) and Pearson (2018).[11]

Dray disagreed with the view that all good scientific explanations must involve laws of nature and held that in historical research modes of explanation were used that did not conform to the covering law model but still constituted good explanations of historical explananda. One such mode of explanation Dray named 'how-possibly explanation'. Dray argued that while covering law explanations show that the explanandum was *necessary* given the circumstances and the applicable law(s), how-possibly explanations show that the explanandum was *possible* notwithstanding that the available information would have us expect that it could not possibly occur. He wrote:

> "An explanation is called for, because we cannot reconcile what we know, or think we know, with an alleged fact [...]. What we know seems to rule out the possibility of the occurrence which is to be explained. The explanation consists in showing that in spite of appearances to the contrary, it is not an impossible one after all." (Dray, 1957: 161).

Whereas covering law explanations rebut the assumption that the explanandum *need not* have happened, how-possibly explanations rebut the assumption that it *could not* have happened (Dray, 1957: 161).

The general structure of how-possibly explanations is as follows. On the basis of available knowledge, we had expected a particular event to occur in a particular way. However, it actually took place in a different, unexpected and unlikely way. The explanandum thus is a contrastive fact: that the event took place in one way *rather than* the expected way. Dray (1957: 158-164; 1968: 390-391) provided a toy example that serves well to illustrate how how-possibly explanations work. In a baseball game a field player caught a ball that would have hit the back fence too high up for him to jump to catch the ball. In this case, however, the ball happened to hit the fence at a location where a ladder was in place leading to the scorekeeper's platform, enabling the player to climb the ladder, step onto the platform and catch the ball. What causes surprise about this event is that the player caught the ball while we expected this to be impossible, because the ball flew too high – the explanandum is how the sequence of events could possibly have occurred in the way it did rather than the way baseballs are usually caught. Dray argued that generalizations about baseball (rules of the game, empirical generalizations of how strikes of this kind typically play out, etc.), laws of nature (e.g., about jumping and reaching capacities of human beings), empirical generalizations about the behavior of rational agents, etc. cannot explain the explanandum. Here, a particular circumstance (a ladder and platform coincidentally being in the right place) is what is doing the explanatory work.

Note two things about how-possibly explanations. First, Dray's argument does not only address the question which kind of explanans is the correct one for the case at hand (local circumstances rather than empirical regularities), but also to the question what the actual explanandum is (not the event itself, but its possibility). Dray's point is that for explananda of a particular kind (phenomena that have a very low to vanishingly small probability of occurring, but occurred nonetheless) a particular mode of explanation must be invoked to explain how it was possible that the

phenomenon occurred notwithstanding its low probability. Second, because this sort of phenomena are precisely the phenomena in focus in evolutionary research, Dray's how-possibly explanations can counter "improbability objections" to evolutionary explanations by explicating how the presence of an ancestral state made the step to a novel state possible.[12] The human eye has not been built from loose parts, for example, but resulted from a long series of small modifications upon small modifications, and so on, in which the step from one state to the next was comparatively easy to realize by natural processes. The sequence of structures that were transformed into new structures is known by comparison: many of the light-sensitive structures that preceded the human eye are still found in extant species with which *Homo sapiens* shares closer or more distant common ancestors (Schwab, 2018). A how-possibly explanation of the human eye thus does not explain the trait, but the possibility of a natural trajectory leading to the trait. This means that to explain the trait, such a how-possibly explanation must be complemented by a processual explanation showing how the human eye actually evolved (which selection pressured operated, whether drift played a role at some stage, etc.).

The explanation-seeking question for how-possibly explanations in evolutionary biology thus is: How could trait or structure *T* possibly have evolved, given that the occurrence of a complex functional entity such as *T* is very improbable? *That* question is answered by explaining that the evolutionary process leading to *T* was possible because there existed a precursor structure *T'*, structurally only a small step away from *T*, such that a natural process could fairly easily transform *T'* into *T*. This does two things: (i) it determines the trajectory from *T'* to *T* as the explanandum for a processual explanation, and (ii) it explains how this trajectory could possibly have occurred in the face of the low probability of evolutionary trajectories in general. In this way, a historical how-possibly explanation by itself explains an important aspect of the existence of *T* that a processual explanation does not explain. The processual explanation (the specification of the *actual* process that occurred during the trajectory from *T'* to *T*, involving selection, drift, or other processes, depending on the case at hand) complements the how-possibly explanation by answering a different explanation-seeking question.[13]

Both explanations are complete explanations of their own explanandum, and neither can by itself be seen as *the* evolutionary explanation of *T*. The evolutionary explanation of *T*, I suggest, consists in the combination of both: the how-possibly explanation shows how the evolution of the trait was possible (and by doing so, why the trait is an explanandum for an evolutionary explanation in the first place), while the processual explanation shows how its evolution actually occurred. What connects the two modes of explanation into an evolutionary explanation is the concept of evolvability, I will now argue.

7 | CONNECTING HISTORY AND PROCESS

The explanatory work of historical how-possibly explanations as parts of evolutionary explanations can be framed in terms of the notion of evolvability, "the robust and abstract dispositional property of populations to evolve" (Brown, 2014: 569).[14] How-possibly explanations (often implicitly) invoke this dispositional property. At the start of the evolutionary process that transformed *T'* into *T*, the dispositional property of the population that made it possible for *T* to evolve (i.e., for the population to take the trajectory that was ultimately taken) consisted in the widespread existence of *T'* in the population as the material basis for further evolution, along with other factors internal to the population. A how-possibly explanation of the trajectory specifies these factors to show how the trajectory was opened up. Let me clarify.

The concept of evolvability underwent considerable meaning change since its introduction in the 1930 s, with many usages involving the ability to generate variation as the material for selection to work with (Crother & Murray, 2019). Although at present the term is used with multiple meanings (Brown, 2014; Crother & Murray, 2019), in its most general sense the evolvability of a population can be seen as covering the various factors *internal* to a population (attributable to a population as an evolving entity) that determine in which directions and at which speed it could evolve from its current state (Brown, 2014; Sterelny, 2007). Evolvability thus can be "used to explain the evolutionary trajectory of populations by capturing the influence that the internal features of populations can have on the outcomes of evolution" (Brown, 2014: 550).

This disposition of a population to evolve in certain directions but not others should be distinguished from the historical conditions (which are *external* to the evolving population) under which the evolutionary process takes place. In this general sense,

> "evolvability is an abstract and robust dispositional property of populations whose physical basis is the many non–selection-based features of populations (such as mutation rate, developmental constraint, and population structure) that can influence the parts of phenotypic space populations are able to access over evolutionary time" (Brown, 2014: 550).

Homology at the structural and genetic level is an important aspect of evolvability in this sense, namely as part of the developmental canalization or generative entrenchment making some evolutionary trajectories possible and others impossible. Other relevant factors are increasingly being taken into account too (Crother & Murray, 2019: 3792), most importantly connected to the current debate on a possible Extended Synthesis. Baedke et al., for example, pointed out that in an Extended Synthesis "processes such as developmental bias, phenotypic plasticity, extra-genetic inheritance, and niche construction should be understood as developmental 'proximate causes' that can direct and facilitate evolutionary change" (2020: 4). The authors observed that such processes do not only constitute explanatory factors in the extended theory, but themselves also constitute new explananda in evolutionary research. The internal factors that determine a population's evolvability themselves are products of evolution (Pigliucci, 2008), and as such are biological phenomena in need of their own evolutionary explanations.

Evolvability thus is at the same time an explanans and explanandum (Brown, 2014: 550, 569). The concept can play this dual role, because it does not refer to a single, concrete property – a population's evolvability supervenes on a multitude of properties of the population as well as its member organisms (Brown, 2014: 561). Evolvability is a disposition rather than a manifest property: because of the chance events determining the actual course of evolution the mere possession of this disposition does not mean that it will manifest itself and the trait will actually evolve. As "an abstract robust disposition of populations to evolve in certain ways" (Brown, 2014: 563; also 566), a population's evolvability at time *t* can explain the possibility of the evolutionary trajectory that was taken from *t* onward. Such evolvability-based explanations, as Brown calls them,

> "explain evolution by reference to the broad internal disposition of a population to evolve rather than for any actual evolutionary trajectory. [...] Evolvability-based explanations refer to differences in the internal (rather than external) features of populations that increase the probability of a particular evolutionary outcome in the

future (for example, adaptedness, diversity). Their general form is as follows: it was, 'selection aside,' more probable that population *x* would evolve the characteristic or characteristics of interest than population *y*. Evolvability-based explanations account for features of the tree of life by considering the role that the internal features of populations can have on the outcomes of evolution. They are also robust-process explanations." (Brown, 2014: 560)

Brown thus locates such explanations on the processual side of evolutionary biology, joining selection explanations in providing an account of the actual process. They explain an aspect of the evolutionary process that selection explanations leave unexplained: while the latter highlight the environmental factors under which evolutionary processes take place, evolvability-based explanations highlight abstract, general dispositions of the populations that take part in these processes.

But ultimately the population's evolvability must itself be explained by specifying its physical basis. Brown (2014: 560) points out that evolvability-based explanations are shallow and must be given more depth by examining details of the population in question and its member organisms. Details regarding population structure, genetic makeup, developmental constraints in the population's organisms, organismal structures, phenotypic plasticity, and so on, must be added to "provide an account of the physical realisers of the disposition (i.e. evolvability)" (Brown, 2014: 561). This, I suggest, is precisely what how-possibly explanations do. They specify how at the start of the evolutionary trajectory from *T'* to *T* the populations' capability for following this trajectory was realized. Recall Dray's example: the how-possibly explanation did not refer to abstract possibilities of a particular course of events, but specified which factors realized the possibility of the course of events before it occurred (the presence of a ladder and platform). By specifying material conditions underlying a population's capacity for taking certain evolutionary trajectories but not others, how-possibly explanations explain a population's disposition for evolving a descendant state from an ancestral state, as well as why this change is an explanandum for a processual explanation.[15]

How-possibly explanations thus explain the dispositions of populations to evolve specific traits by highlighting factors internal to populations that obtained at a point in their evolutionary histories, making future trajectory possible. But this is only part of what how-possibly explanations do. They are not limited to specifying internal factors, but can also specify historical circumstances external to evolving populations that open up particular evolutionary trajectories. (Dray's ladder and platform, after all, were environmental circumstances.) Both kinds of factors perform genuine explanatory work: external factors explain why a particular evolutionary trajectory (with very low probability) is open to a suitable population, while internal factors explain *why a given* population is suitable to actually follow that trajectory. How-possibly explanations thus have a broader explanatory reach than Brown's evolvability-based explanations, and provide a foundation for the latter.

Because of their dependence on historical how-possibly explanations, evolutionary explanations are recursive: the evolutionary explanation of *T* involves a how-possibly explanation citing the existence of *T'* as explanatory factor, but as *T'* itself is a trait in need of an evolutionary explanation, there must be an evolutionary explanation of *T'* that involves a how-possibly explanation citing the existence of *T''* as explanatory factor, and so on. A full account of the evolution of *T* thus would encompass a multitude of – by themselves complete – evolutionary explanations of sequential stages. This is not a weakness of evolutionary explanations – it is part of any study of the products of a long history of accumulated change.

8 | THE PROPER ROLE OF HISTORY IN EVOLUTIONARY EXPLANATION

Let me now return to the question alluded to in the title of this paper: What is the proper role of history in evolutionary explanations? Evolutionary stories tell us how a particular process under certain conditions yielded a particular explanandum. Gould and Lewontin criticized such stories, arguing that they can easily misidentify the explanandum, the explanans, or both, while still being plausible stories that are indistinguishable from adequate scientific explanations. Orzack and Sober agreed and proposed a solution, noting that such stories by themselves are not testable but can be made testable by adding a historical component in the form of assumptions about common descent. This approach treats such stories as *potential explanations*: they might be correct and we can use history to assess their correctness.[16] The historical part of evolutionary research is here treated as providing the initial conditions for the processual part. Griffiths (1994; 1996), too, highlighted this by arguing that evolutionary explanations should be both adaptive and historical (see also Wagner, 2014: 425), seeing history as providing initial conditions for adaptive explanations. But this approach only acknowledges one part of the role of history in evolutionary thinking and misses a large part of the role of history.

Biologists and philosophers of biology have long recognized another role of history in relation to the concept of homology (e.g., Ereshefsky, 2009; 2012; Wagner, 2016). Identifying traits in different lineages as homologues amounts to individuating traits as explananda, but also to explain them by providing information about ancestral states as well as major trait changes on the way to end states. Applying such "homology thinking" (as Ereshefsky calls it; see also Wagner, 2016), one "cites a character's history to explain its properties" (Ereshefsky, 2012: 382). More precisely, the state of a trait or the range of variation in trait states is explained by explicating what ancestral state it evolved from and/or what steps occurred in the evolutionary trajectory that led from the ancestral to the descendant state (Ereshefsky, 2021: 388-390), i.e., by "citing either an initial condition or a series of events in the history of a homologue" (Ereshefsky, 2012: 397). Ereshefsky contrasts such explanations with adaptive explanations and argues that sometimes historical explanations explain traits better than adaptive explanations. On Ereshefsky's view, history provides initial conditions and specifications of states of affairs at certain stages in the evolutionary process, which he takes as explanatory. However, as I argued in Section 3, *only* invoking history amounts to giving merely partial evolutionary explanations. History explains how the trait *could possibly* be present in a current population: starting from an ancestral state and a specific environment, either this state was retained to the present, or a series of modificatory steps occurred, each making the next step possible. But this does not explain how it *actually came to be* present, i.e., why it actually was retained or why the sequence of modificatory steps actually occurred.

In contrast to Orzack, Sober, and Griffiths (and in alignment with Ereshefsky), I have argued that history does more explanatory work than just providing initial conditions for adaptive explanations, and is explanatory by itself. In contrast to Ereshefsky, however, I have argued that history on its own does not fully explain traits but accounts of both history and process, joined into evolutionary explanations, are required.[17] The proper role of history follows from the fact that evolutionary biology has a dual nature: it is an empirical natural science, while at the same time being a thoroughly historical science too. In the "natural science part" (processual part), the principles of selection, drift, and other evolutionary processes describe general aspects of evolving systems independently of their concrete (biological as well as non-biological) material instantiations, in the same way as for example Maxwell's equations describe general features of electromagnetic

phenomena independently of their material instantiations. This processual part of evolutionary biology resembles other experimental sciences in the way in which it accounts for the phenomena under investigation: it does so by referring to one or several general processes (most importantly, but not limited to, natural selection) that produce these phenomena (most prominently, but not limited to, organismal form and adaptation, organismal diversity, and trait distributions). Similarly to the other experimental natural sciences, these processes can be studied in nature as well as the laboratory. Natural selection processes, for example, can be systematically studied in the wild (Endler, 1986), in controlled experiments in natural populations in the field (Reznick & Ghalambor, 2005), in laboratory populations of living organisms (Reed & Reed, 1948; 1950) and in *in silico* populations of digital "organisms" (Lenski et al., 2003). When considering *only* the processual part of evolutionary biology, Orzack and Sober are right to say that historical comparisons provide information about initial conditions that enables the testing of process hypotheses. But this is a non-explanatory role of history.

My point was that there is much more to evolutionary biology than testing of processual explanations. Well-tested processual explanations are not the same as evolutionary explanations and, *pace* Orzack and Sober, history is required for more than just hypothesis testing. The historical part of evolutionary biology complements and supports the processual part in several ways besides making process hypotheses testable: by determining the ancestral state and thus which evolutionary trajectory was taken, and subsequently specifying environmental factors as well as factors internal to the evolving populations that obtained at the start of the evolutionary trajectory, history explains how the processes described in the processual part were possible.

Summarizing, I suggest that the proper role of history in evolutionary explanations is fourfold:

1. Assumptions about common descent render process explanations testable by enabling comparisons between species of evolutionary trajectories.
2. Assumptions about common descent fix the explanandum of processual explanations by explaining why the evolutionary trajectory under consideration is an explanandum for a processual explanation in the first place. (Short answer: it is an explanandum because it occurred in one lineage but not in other closely related ones.)
3. Specifying environmental conditions at the start of the evolutionary trajectory constitutes one part of a how-possibly explanation that explains how the trajectory was possible (notwithstanding its low probability). These factors can be understood as initial or boundary conditions, but I have argued that (in contrast to the model of DN-explanations) they are explanatory.
4. Specifying factors internal to the evolving population explains the population's evolvability and constitutes the other part of the how-possibly explanation of the evolutionary trajectory.

Together, these four roles provide what Gould and Lewontin called the "key to historical research, [...] criteria to identify proper explanations among the substantial set of plausible pathways to any modern result" (1979: 588).

Distinguishing these four roles allows us to see why the how-possibly explanation does not become obsolete once a processual explanation has been formulated that explains how the evolutionary process actually occurred. Rosenberg (2006: 43-44; 2007: 360) suggested that this was the case – that once it has been shown how an event actually happened this directly entails the event's possibility and thus makes any how-possibly explanation superfluous. But this misses the full spectrum of what how-possibly explanations explain. Rosenberg's claim latches onto role 3 of how-possibly explanations: once a complete processual explanation including the relevant initial conditions has been formulated, the how-possibly explanation playing role 3 becomes absorbed

into the processual explanation and indeed becomes obsolete. But this misses roles 2 and 4 of how-possibly explanations, specified above, which do not become absorbed into processual explanations as they address non-processual aspects of evolutionary history (i.e., why a trajectory is an explanandum for a processual explanation and why it was possible for a population to embark on the process that the processual explanation describes). How-possibly explanations have more explanatory work to do than staunch reductionists like Rosenberg think.

In the same way as evolutionary biology has a dual nature, evolutionary explanations have a dual nature: they encompass a processual part and a historical part, each providing its own type of explanation of its own kind of explanandum. The historical and processual parts (the latter often taking the form of adaptive explanations) are not alternative explanations. Only the two explanations jointly explain the explanandum in focus in a proper evolutionary sense, I suggest, and the connection is provided by the concept of evolvability.[18] In other words: *Evolutionary explanations constitute a genre of explanations that are composed of two other kinds of explanation, namely a processual explanation (a description of how the evolutionary process actually played out, invoking the regularities of evolutionary theory as its explanatory core) plus a how-possibly explanation (a historical description of factors that made the occurrence of the process possible in the first place). The how-possibly explanation is what transforms a merely plausible evolutionary story into an actual evolutionary explanation.* As the historical how-possibly explanation is comparative in nature and evolutionary explanations are composites of two modes of explanation, I call this general mode of explanation, of which evolutionary explanations are instances, *comparative-composite explanations.*

The comparative part of evolutionary explanations serves to mitigate the explanatory risks highlighted in Section 3. It does so at the price of raising a new explanandum (the evolutionary trajectory's possibility) that in turn is explained by the how-possibly explanations contained in evolutionary explanations – hence the need for evolutionary explanations to be composite. The explanatory risks occur because in the process-oriented part of evolutionary biology the phenomena by themselves underdetermine which explanatory factor(s) should be invoked. Comparisons between taxa help researchers individuate explananda and see the connections between traits and possible evolutionary trajectories more clearly, and to cull the plethora of possible process stories.

Note that I did not present an account of evolutionary explanations as a homogeneous category of scientific explanations. The technical term 'evolutionary explanation' does not denote a homogeneous kind of explanation, but what I have called a genre of explanation – a way of explaining that always involves a historical and a processual explanation, but in which different kinds of historical and processual explanations will have to be invoked for different cases. I presented a reconstruction of the coarse-grained structure of evolutionary explanations, showing how their parts do explanatory work. At a more fine-grained level, it still has to be explicated how the various modes of explanation mentioned at the beginning of this paper can play roles within the overarching structure presented here. I suggest that these can be flexibly plugged into this structure. For example, selection explanations and evolvability-based explanations will often play important roles in the processual part of evolutionary explanations, while for some traits topological explanations presumably can feature as part of the how-possibly part. While all conform to the same overarching structure of comparative-composite explanations, concrete evolutionary explanations will differ considerably between cases, allowing for considerable explanatory pluralism in evolutionary biology.

The reconstruction presented here is an *ideal model* that actual explanations in evolutionary research approach to some degree. Because of the gappiness of available knowledge about natural history on planet Earth, often the ideal will not be fully achieved. Also, we don't typically find

complete evolutionary explanations in the sense described here in research papers in evolutionary biology: research articles typically focus on only part of the whole story and complete evolutionary explanations are spread out over multiple publications. Still, as a model of how evolutionary explanations work it accounts for the explanatory success of evolutionary biology. And I think it can serve as a heuristic for evolutionary research by specifying the overall explanatory structure that researchers should aim to realize – even if in practice it might not be a fully achievable ideal. The structure of evolutionary explanations sketched in this paper can thus be thought of as a general goodness criterion for evolutionary explanations: I have presented a – admittedly somewhat coarse-grained – sketch of what overarching components a good evolutionary explanation should consist of and how these components should be connected.

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ENDNOTES

[1] For a similar view, see Tennant (2014).

[2] Jackson and Pettit (1992) advocated a similar "explanatory ecumenism" for scientific and everyday explanations more generally, noting that phenomena generally are susceptible to a range of explanations ranging from very fine-grained to very coarse-grained explanations.

[3] In Sections 5–6 I will develop precisely this point: both kinds of explanation are needed for complete evolutionary explanations. An anonymous reviewer commented that sometimes history *does* provide the explanation we are looking for: when we ask why trait similarities are found in organisms of one or multiple species, saying that they inherited them from a common ancestor seems to adequately explain the similarity by specifying its cause (inheritance from a common ancestor). I disagree. I think history is always part of the explanation, but it never is the full explanation. History explains how a trait *could* be retained as an ancestral state but not why it actually *was* retained. In other words, when asking why a particular trait occurs in organisms of one or multiple species, we cite history to show that at some point in time there was an ancestral state that could either be retained in subsequent evolution or transformed into different states in different descendant groups. We then cite the evolutionary process that actually occurred to show that this ancestral state was retained (e.g., due to stabilizing selection (Griffiths, 1996: 524-526) or pleiotropy) rather than transformed or having become vestigial. Ancestry thus is half of the picture: it tells us what existed at some point in time for evolution to work with. The actual evolutionary process is the other half: it tells us why the ancestral state was retained. For more details, see Sections 5-6.

[4] Holton et al. (2015) add to this evidence by rebutting the "bending stress deflection" hypothesis by means of a biomechanical and ontogenetic analysis.

[5] While Sober and Orzack conceptualize this in terms of heritability, in Section 7 I will argue that it is better conceptualized in terms of the concept of evolvability rather than heritability.

[6] "Current fitness is not necessarily indicative of past selection of course, but it is a common assumption in behavioural ecology and evolutionary anthropology." (Waller et al., 2013: 1).

7 See Novick and Scholl (2020) for a thorough discussion of the *vera causa* ideal in the life sciences.

8 See also Darwin (1859: 479) for explicit discussion of the explanation of homologues by descent. See Waters (2003) for a deeper analysis of Darwin's argumentation in the *Origin* on the basis of the *vera causa* ideal.

9 Currie (2021) recently developed a similar idea with his notion of evolutionary profiles, pointing out that "comparative thinking critically involves the integration of both ancestry and adaptation" (2021: 6). Note, though, that Currie did not provide an account of the explanatory nature of the historical part of evolutionary explanations (which, as I argue, are how-possibly explanations) or of the explanandum of historical explanations in evolution (which, as I argue, is the possibility of an evolutionary trajectory), nor did he seem to consider history to be explanatory in its own right.

10 The notion of generative entrenchment refers to the fact that natural selection builds new structures upon ones that already exist (Wimsatt, 2015: 384). Because of this, the latter structures become more deeply entrenched in the overall structure: they become more difficult to remove, because other structures rest on them. At the same time, they more strongly determine future evolutionary trajectories, both in a negative (constraining) and positive (enabling) manner. The generative entrenchment of a part of an organismal structure is the degree to which that part affects organismal development as well as the evolution of novel structures (Wimsatt, 2001: 220-221; also 2007: 133ff.). As Griffiths (1996: 527) recognized, "[t]he existing developmental system of the organism comes to shape the space of possibilities available to the organism."

11 As an anonymous reviewer remarked, my account can be interpreted as emphasizing the role of history in explanatory evolutionary narratives. Indeed, Dray's how-possibly explanations are instances of the more general class of narrative explanations. But this is an aspect of my account that I am unable to explore here and must be left for future work, both for reasons of space and because my focus here is not on narrative explanation as a mode of scientific explanation. For recent literature on narrative explanations with points that connect to the present paper, I refer to Beatty (2016; 2017), Swaim (2019), and Ereshefsky and Turner (2020).

12 See also the discussion of Ereshefsky's "homology thinking" in Section 7, below.

13 Pearson (2018) recently identified yet another explanatory role of Dray's how-possibly explanations in developmental biology, where how-possibly explanations use models of developing systems to explain the possibility of particular explanatory strategies. For reasons of space, I cannot address Pearson's claim in detail, but want to note that this is a very different kind of explanation from the one I highlighted here.

14 Or, more strictly formulated, "the evolvability of a particular population at a given time is a measure of their capacity to change over time with respect to some future state, given some starting state of affairs." (Brown, 2014: 564).

15 Without specifications of the "realisers of the disposition", a population's evolvability still can do some work, albeit not itself explanatory. If we know that populations have highly similar evolvabilities because they are closely related, we can compare them with respect to the external factors affecting their evolutionary trajectories and test potential processual explanations. To do this, we do not need to know actual values for the variable 'evolvability' for the populations, but only that the comparative differences in these values are small because the material basis for further evolution is highly similar. In terms of evolvability, then, Orzack and Sober's point (Section 4) is that evolving populations sharing close common descent will strongly resemble each other in the factors underlying their respective evolvability, such that differences in their actual evolutionary trajectories can be attributed to external factors, allowing testing of adaptive explanations.

16 Note that contrary to the complaint, sometimes voiced by opponents of evolutionary thinking, that evolution merely tells "just-so stories", this entails that good stories are epistemically legitimate. I will not pursue this point here, but see e.g., Lennox (1991).

17 For a similar criticism of Ereshefsky's view, see Currie (2021: 29). Also, my account of history as providing how-possibly explanations shows in what way the "initial condition or a series of events in the history of a homologue" mentioned by Ereshefsky (2012: 397) perform their explanatory work.

18 Gould and Lewontin (1979: 584, 594) argued for the primacy in some cases of historical constraints over selection. My view contradicts theirs on this point, as I think neither of the two component explanations has primacy. Any good evolutionary explanation needs both.

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