

Please cite as: Veit, W. (2022). Complexity and the Evolution of Consciousness. Preprint.

Check www.walterveit.com for citation details once published

Complexity and the Evolution of Consciousness

Walter Veit¹

School of History and Philosophy of Science, The University of Sydney
Department of Psychology, University of Cambridge

Abstract

This article introduces and defends the ‘pathological complexity thesis’ as a hypothesis about the evolutionary origins of minimal consciousness, or sentience, that connects the study of animal consciousness closely with work in behavioural ecology and evolutionary biology. I argue that consciousness is an adaptive solution to a design problem that led to the extinction of complex multicellular animal life following the Avalon explosion and that was subsequently solved during the Cambrian explosion. This is the economic trade-off problem of having to deal with a complex body with high degrees of freedom, what I call ‘pathological complexity’. By modeling the explosion of this computational complexity using the resources of state-based behavioral and life-history theory we will be able to provide an evolutionary bottom-up framework to make sense of subjective experience and its function in nature by paying close attention to the ecological lifestyles of different animals.

Keywords: evolution of consciousness; sentience; common currency; affective neuroscience; decision theory; comparative neuroeconomics

Index

1	Introduction	2
2	Reverse-Engineering Consciousness	4
3	The Cambrian Explosion in Pathological Complexity	14
4	Conclusion and Further Objections	26

¹ wrwveit@gmail.com; <https://orcid.org/0000-0001-7701-8995>

Complexity is worth caring about, but not just any complexity.

– Daniel C. Dennett (2017)

1 Introduction

The question of how animal consciousness should be studied has remained a controversial one (Birch et al. 2022). Nearly everyone will agree that consciousness has *something* to do with the complexity of organisms², which makes this link worth exploring. After all, it is the complexity of cephalopods that has gained them a lot of recent attention in calls to recognize their sentience, and include them in animal welfare legislation (Fiorito et al. 2014; New England Anti-Vivisection Society et al. 2020; Schnell et al. 2022; Birch et al. 2021). To make this intuitive link useful for science, however, we need to provide a naturalistically satisfactory answer to the question of what kind of complexity is *worth caring about*. A biological science of consciousness must ultimately address the *teleonomic question* of what consciousness does *for* healthy agents within their normal ecological lifestyles and the natural environments they have evolved in.³

This article proposes an answer to this question and a thesis for the origins of consciousness that synthesizes evidence from ecology, neuroscience, economics, and evolutionary biology. The thesis is this:

Pathological Complexity Thesis:

The function of consciousness is to enable the agent to respond to pathological complexity.

Before we move towards a detailed defense of this thesis, let me offer a brief sketch of the pathological complexity thesis and its central concept.⁴ Pathological complexity emerges dynamically from the interaction of organism and environment, as a measure of the complexity of an organism’s *life-history strategy*, and will hence vary with the different ‘lifestyles’ of different animals. It can be understood as the computational complexity of the Darwinian, or ‘economic’, trade-off problem faced by all biological agents as they deal with challenges and opportunities throughout their life histories in order to maximize their fitness. As I shall argue in this article, consciousness evolved in the Cambrian explosion alongside a new evaluative animal *lifestyle*

² Even if they restrict consciousness only to beings as complex as us.

³ By ‘teleonomic’ I am employing Pittendrigh’s (1958) coinage of the term, as a naturalistically unproblematic Darwinian replacement for older and mistaken teleological notions about the purposefulness, design, and normativity of life.

⁴ See also Veit (2022b) for an extended treatment of the pathological complexity thesis.

characteristic of large parts of the Metazoan branch of life. Consciousness is an adaptive response to a computational explosion in just this kind of pathological complexity, due to an increase in degrees of freedom⁵ of Cambrian organisms that made consciousness worth having and led to a major transition in evaluative agency or, as I shall call it, the evolution of *Benthamite creatures*.

Instead of locating the origins of consciousness in sensory experience or self-awareness, as is typical in much of the thinking about human consciousness, the pathological complexity thesis seeks to develop an alternative model of consciousness based on a model of *animal sentience*. Because of the associations of the term ‘consciousness’ with the complexity of the human mind, the term ‘sentience’ - coming from the Latin verb *sentire*, i.e. ‘to feel’ - is often preferred among those with a primary interest in animal consciousness.⁶ The term has not received universal endorsement, however, because it is often used ambiguously as (i) a deliberately broad and inclusive concept to refer to all kinds of subjective experiences, (ii) a reference to the most minimal kind of subjective experience found at the evolutionary origins of consciousness, or (iii) the hedonic capacity to feel pleasure or pain.

Here, we can avoid these ambiguities because this article will explicate the concept of sentience in terms of a unification of all three interpretations.⁷ The origins and *raison d’être* of consciousness lie in hedonic evaluation or ‘valence’ (good, neutral, or bad). This inherently dynamic dimension of consciousness will enable us to build a Darwinian bottom-up model for the function of consciousness and provide a framework to understand the heterogeneity of subjective experiences. As I will argue here, the explosion of pathological complexity in the Cambrian led to the evolution of a proximate ‘common currency’ for efficient decision-making that allowed for fitness-maximizing action-selection by assigning values to competing actions that can be compared and traded-off on a common scale of hedonic valence.

Importantly, I use the term ‘pathological complexity’ instead of the equally adequate and perhaps less confusing terms ‘teleonomic complexity’ or ‘life-history complexity’, not because I want to make the argument that organisms with greater life-history complexity are less healthy, but because I want to emphasize that it is only in understanding life-history trade-offs that we can distinguish healthy from pathological trait variations and that includes variations of consciousness both within and across species (see also Veit and Browning forthcoming b). Nevertheless, the evolution of consciousness - similar to the evolution of behaviour - gives rise to a

⁵ That is, roughly how many alternative actions an organism can take.

⁶ See Browning and Birch (2022) for a recent review of animal sentience research.

⁷ We are not here engaged in a conceptual analysis, but rather a conceptual engineering project to make the notion useable for the science of consciousness, though this unified understanding of sentience is admittedly also engineered to serve animal welfare and ethics (Veit and Browning 2020b).

new adaptive domain in which a pathological mismatch can arise between the evaluations of an organism and what is important from the perspective of biological fitness. Pathological complexity can be operationalised in terms of the number of parameters and constraints in the evolutionary optimization problem studied by *state-dependent or state-based behavioural and life history theory*. This will offer us an elegant mathematical framework to naturalize the idea of a distinctive ‘animal lifestyle’ central to an understanding of hedonic evaluation as a proximate real psychological utility that helped organisms to maximize their fitness during the Cambrian explosion.

Article Outline

This article is organized into two main sections. In Section 2 ‘Reverse-Engineering Consciousness’, I address the objection of why it should be pathological complexity, rather than any other measure of complexity, that should matter for the evolution of consciousness. In Section 3 ‘The Cambrian Explosion in Pathological Complexity’, I seek to locate the origins of valence in the computational explosion of pathological complexity during the early Cambrian. Finally, Section 4, ‘Conclusion and Further Objections’ will summarize the main arguments and respond to potential objections.

2 Reverse-Engineering Consciousness

In trying to reconstruct the possible evolutionary origins and function of consciousness, we are engaged in the paleobiologist’s effort of making sense of a trait by connecting its extant ‘users’ with its historical traces. When we think about hedonic valence in humans, it is choices, desires, motivation, and preferences that come to mind; and it is the evolution of such capacities related to action that we will have to pay attention to if we want to understand the evolution of sentience.

One important figure, who has attempted to develop a plausible natural history of the evolution of human agency and cognitive states resembling the standard folk-psychological states of belief and desire, has been Sterelny (2003). Unfortunately, his work has paid comparatively little attention to the latter. This has been criticized by Spurrett (2015) whose thinking about the evolution of desire-like states and preferences had major influence on my thinking here.⁸ Both Sterelny and Spurrett draw on the ‘ancestor’ of the pathological complexity thesis to make sense of the evolution of preferences. Godfrey-Smith’s (1996a) *environmental complexity thesis* was an attempt within the modern framework of evolutionary theory to make tenable earlier ideas from John Dewey and Herbert Spencer about the continuity between life and

⁸ We have also collaborated on this topic (Veit and Spurrett 2021).

mind; the mind seen as a natural consequence of the evolution of biological complexity.⁹

Unlike Spencer and Dewey, however, who intended to include consciousness in their explanation of mental complexity in terms of biological complexity, Godfrey-Smith restricted himself to explaining only basic cognitive capacities, excluding subjective experience. While the pathological complexity thesis differs both in its explanandum and explanans, it is nevertheless indebted to the elegant explanatory framework and naturalist ambition of Godfrey-Smith's thesis: "The function of cognition is to enable the agent to deal with environmental complexity" (1996a, p. 3). However, we may well ask whether we could use the environmental complexity thesis to explain the evolution of valence if it is being used to explain the evolution of desire-like states. Why is it pathological complexity, rather than environmental complexity, that matters for the evolution of consciousness?

While the environmental complexity framework has an explicit link to action, it was (at least originally) designed as an externalist theory, i.e. it was meant to explain organismal features through recourse of properties external to the organism, rather than ones internal (Godfrey-Smith 1996a). It thus in that respect shares more with Spencer's externalism than it does with Dewey, who saw the complexity of the mind as something that evolved to deal with problems emerging in the dynamics between organism and environment, which in turn is closer to the pathological complexity thesis. So it should not be surprising that explications of the environmental complexity thesis have tended to pay very little attention to the organism as a "design and control architecture", instead treating the mind as something that decides what to do with the body conditional upon a given external state of the world (Spurrett 2020, p. 5). While I am here largely concerned with consciousness, rather than cognition, the two are tightly linked and so it is perhaps unsurprising that I resist such a strongly externalist picture for cognition as well as for consciousness.

To emphasize the importance of not tying an adaptationist viewpoint too closely together with an externalist perspective, it is useful to draw on a largely inverse version of Godfrey-Smith's environmental complexity thesis, that been popularized in a series of publications by the Fred Keijzer (Keijzer 2015; Keijzer et al. 2013). Whereas Godfrey-Smith's account of the origins of cognition largely idealizes the organism away and has been influenced by the externalist strategies of behavioural ecologists and evolutionary biologists two fields with a history of black-boxing the internal goings-on of organisms - Keijzer's approach is strikingly internalist and focuses on the nervous system and work in developmental biology. Keijzer et al. (2013) propose that the early function of the nervous system was to enable action "as a *single multicellular unit*" (p. 68), rather than to deal with incoming sense-data. For Keijzer, the popular input-output story is relatively unimportant when we are

⁹ See also Godfrey-Smith (1996b,c, 1997).

concerned with the evolutionary origins of the nervous system, which he suggests plays the role of coordinating the body irrespective of what goes on outside, going hand in hand with the evolution of contractile tissue (muscle) close to the skin or epithelium of an animal. Borrowing the term “skin brain” from the developmental biologist Nicholas Holland (2003), Keijzer et al. (2013) call their hypothesis the *skin brain thesis*. The nervous system, they argue, evolves in order to solve a non-trivial control problem at a multicellular level, that has to be re-invented at this new scale of biological organization.

In a later paper, written as a direct response to Godfrey-Smith’s earlier work, Keijzer and Arnellos (2017) explicitly describes his skin brain thesis as an *internal complexity proposal*. While they don’t use the reverse title internal complexity thesis, they get quite close: “acquiring the fundamental sensorimotor features of the animal body may be better explained as a consequence of dealing with internal bodily—rather than environmental complexity” (p. 421). They consider the fundamental design problem one of motility, where nervous systems had to evolve to allow for the coordination of an organism’s body, which they think must have evolved “long before the Cambrian Explosion” (Keijzer and Arnellos 2017, p. 424). But while they are certainly on to an important transition in the evolution of multicellular life, their approach is limited by a deliberate resistance to externalist thinking about the role of cognition in interactions of the organism with its environment, though it perhaps provides a useful antidote to an excess of these externalist ways of thinking in the study of the brain.

However, my goal in providing a brief exposition of these views was not to argue that one is right whereas the other must be wrong. Despite the apparent conflict between these views (not unaided by the competitive responses to each other’s proposals), one need not necessarily see them as competitors. Both may capture important aspects of the phenomenon we call ‘cognition’ and thus a more pluralist, or rather integrative, approach may be worth pursuing here. Spurrett (2020), for instance, argues that we could see them as two versions of a more general view, merely differing in their emphasis. But what would a general version of such a view imply? A complexity thesis? This much, we already knew. Complexity, as Dennett nicely emphasizes in my epigraph, matters - but what makes it matter? What is it that makes it useful to respond to internal or external complexity? Spurrett (2020) proposes a “friendly amendment of the ECT” that takes into consideration both internal and external sources of complexity: “The function of cognition is to enable the agent to coordinate its (possibly complex) capacities, which can include coordinating those capacities with environmental complexity” (p. 5). But this loose definition only takes us half of the way.

It is simply not enough to describe what cognition does on a general level. Like Dennett (2017, 2018), we should ask the hard question: and then what happens? Why coordinate? Why act? As we’ve seen with the ECT, it cannot be complexity *per se*. In

more recent reflections on his earlier work, Godfrey-Smith (2017) admits that he was overly eager to state the environmental complexity thesis in externalist terms and recognizes that it isn't environmental complexity, *per se*, that matters, but rather the complexity faced *by* and mattering *to* organism. Here, we ought to reject the dilemma between externalism and internalism. Indeed, in his recent work Godfrey-Smith (2020) acknowledges the influence of Keijzer in his rejection of mainstream externalist representationalist thinking in the philosophy of mind, describing his ideas as an “emphasis on the *shaping of action*” (p. 59) that is so important if one wants to understand the branching of an animal *way of life*.¹⁰

The origins of mind lie in the control of action, rather than as a sensory detection-system, and a Darwinian approach to the mind must emphasize feedback between features of the organism and environment, since it is here that we see a dynamic emergence of a kind of complexity that *matters* for a teleonomic system. It is this teleonomic complexity that I call ‘pathological complexity’, and it can be understood in terms of the life-history strategy of the organism. Features such as environmental and bodily complexity must be seen as variables that are relevant for the pathological complexity of an organism - they may be sources for it - but in asking for the complexity that matters to the organism, we must ultimately focus on pathological complexity as *the* teleonomic measure of biological complexity.

Pathological Complexity and the Need for Valence

The pathological complexity thesis maintains that the function of consciousness is to enable the agent to respond to pathological complexity, which is the economic trade-off problem faced by all organisms in the pursuit of their teleonomic goal of maximizing fitness. The ethologist and animal welfare scientist Marian Dawkins perhaps came the closest to articulating the kind of complexity thesis that I have in mind. Consider the following illustrative quote:

Animals usually have more than one kind of danger to avoid. They have *complex tradeoffs* at all levels in order to minimize reductions of fitness in facing a wide range of threats. At different times of the day or year, or depending on external circumstances, they will reallocate priorities: For example, animals may depress or enhance their immune responses, increase or decrease their physiological “stress” responses, or find some stimuli more or less aversive.

– Marian Dawkins (1998, p. 322) [italics added for emphasis]

¹⁰ By representationalist approaches in the philosophy of mind, I mean attempts to understand and distinguish mental states in terms of their fit to an external world.

Like our focus here on evaluative feelings, Dawkins (1998) suggested early on that the very “key to the origin of consciousness itself may lie in the emotional experience of suffering” (p. 324). Notice that Dawkins speaks here of an experience *of* suffering - by which she means physical suffering in the sense of bodily ill-health - rather than suffering *as* a mental experience, suggesting that for her, consciousness evolves first and foremost to respond to threats to health.¹¹ Trained as an ethologist under Tinbergen at Oxford, Dawkins has been one of the most fervent critics of the lack of evolutionary thinking within animal welfare science. In an influential paper in *The Quarterly Review of Biology* with the title ‘Evolution and Animal Welfare’, Dawkins (1998) argued that to truly understand the welfare and subjective experience of animals we must use an evolutionary approach, just as we would for any other biological phenomenon: “[a]nimal welfare, in other words, needs a dose of Darwinian medicine (Nesse and Williams 1995)” (p. 305).¹²

That there could be a strong evolutionary link between physical and mental suffering has long been a central tenet of those working in the sphere of Darwinian medicine. Nesse and Williams (1995), for instance, argued early on that some of the emotional states we disvalue and consider to be indicative of poor wellbeing - such as pain and fear - are evolutionary adaptations that are “unpleasant by design” (p. 26). Consciousness itself can be seen as such an adaptation to ensure the health of the organism. Evaluative agency evolved in order to deal with the economic decision-making trade-offs of animal life. What Dawkins (1998) highlights is the need to recognize a teleonomic notion of “complexity of an animal’s adaptive response to various dangers” (p. 322), to which one should also add opportunities. Just like life is an evaluative and goal-directed activity, so is consciousness an evaluative and goal-directed way of engaging with the world, evolved within the context of life. It has evolved in order to respond to pathological complexity, which includes both opportunities *and* problems - such as the possibility of a common brushtail possum (*Trichosurus vulpecula*) stealing an unsupervised fledgling from a nest. What presents an opportunity for the possum also presents both a problem and a danger to the chick.

But we need to be careful not to become too tempted by the representationalist modes of thinking that turned the sensory side of subjective experience into the mainstream model for consciousness. Despite his earlier criticism of the environmental complexity thesis for tying adaptationism and externalism together,¹³ Sterelny (2003) maintains that the environmental complexity thesis offers us something like a useful coarse-grained abstraction for investigating the origins of desire-like states. This is largely explained by his interest in the evolution of proto-

¹¹ I have argued elsewhere, that such a purely naturalist sense of health can be defended (Veit 2021b,d; Veit and Browning 2021c).

¹² See also Veit and Browning (2021a).

¹³ See Sterelny (1997).

representational states, which makes him at least in this sense firmly connected to older mainstream representationalist thinking in the philosophy of mind. Spurrett (2015) likewise operates in an representationalist model of the mind and considers the evolution of preferences and common currencies as value representations, but he also recognizes that the problem of coordinating the body around action is a very difficult and much neglected problem.

What I want to highlight, however, is that is a mistake to tie the origins of valence together with the origins of representational richness, since to do so underestimates the importance of efficient decision-making and action control for any system with high degrees of freedom. Valence is plausibly much simpler than a rich representational capacity, arising as something very primitive, but not so simple as to make it a default for all evaluative processes of life. By taking a design stance - i.e. by explicating the pathological complexity of different organisms and thinking about the properties that would make valence worth having - it is easy see which properties would be relevant. Vulnerability and mortality *matter*. If a system is 'indestructible' and almost immune to dangers posed by its environments, there is little sense in demanding pain. Autonomy and sufficiently flexible behaviour likewise *matter* because valence evolved to deal with the complexity of choice-problems and action selection. Furthermore, a system that cannot respond adequately to dangers or injuries does not appear to require the machinery for evaluation. All of these facts are hardly surprising - they are generally accepted by many in the debate, and beautifully expressed by Dennett:

The complexity of an autonomous, self-protecting, self-advancing (but mortal, vulnerable) bit of machinery gives us an explanation of why it is equipped to suffer, and why its suffering matters *to it*.

– Daniel Dennett (2017) [italics added for emphasis]

Such a capacity for negative valence has little to do with representing the world, even internal states, and much more with enabling efficient adaptive behaviour. The task of the pathological complexity thesis must be to turn this vague, but popular idea into a precise scientific hypothesis and a framework for an ethological study of consciousness.

How organisms ought to deal with their species-specific pathological complexity can be explicated in terms of a unified teleonomic state-based and behavioral life history theory of organisms, that accounts for all the actions an organism can take. But Mangel and Clark (1986) rightly note that anything like a unified foraging theory will become almost impossible to assess, since “more complex models can rapidly become computationally unwieldy” (p. 1135). Typically, behavioral ecologists constrain the option-space of the different actions organisms can take to a manageable set. But this is simply an idealization to make the life-history

trade-offs manageable within a model. Once organisms can take alternative actions that change their place in nature, we are faced with a dynamic programming problem, and “[i]t is well known that dynamic programming problems become computationally infeasible as their dimension increases” (Mangel and Clark (1986), p. 1128). We are faced with a combinatorial explosion in trying to model the optimal life history strategies for organisms with high degrees of freedom. But the very reason it is so hard to model the maximization problem of their life-history strategy, is precisely why valence evolved as a proximate common currency for action selection that reflects the fitness values of alternative actions.

Importantly, pathological complexity is an optimization problem for organism and modeller alike: it is the complexity that matters for the *organism* both in the sense of an object and a subject of evolution. Within biology, some types of dramatically fluctuating environments are thought to favor very simple organisms: if it is very hard to survive bad seasons, the best option may be to have a capacity to reproduce very quickly when times are good (Bonner 1988, p. 49). Godfrey-Smith’s environmental complexity thesis neglects this: one way to deal with environmental heterogeneity is to become simpler and thus to reduce the *pathological complexity* an organism has to deal with. To idealize away important features of the internal complexity of organisms in the context of understanding the function of mind forces us to neglect some of the most important features of what makes an organism both an object and subject of evolution. In order to understand these complex dynamics of a teleonomic system, a state-based approach is needed, that pays attention to both internal and external features of an organism.

If we follow the ethologists’ demand to study adaptive value alongside of mechanisms and developments, we must answer the black box problem of how organisms optimize their behaviour. How organisms ought to deal with trade-offs between different goals is in principle no different from how we think conscious agents ought to resolve their conflicting goals. As Okasha (2018) notes, agency in folk psychology, economics, and evolutionary biology requires *unity of purpose*, or at least consistency among goals. We can usefully describe a system as an agent if there is a goal that all the processes and mechanisms work towards (see also Veit 2021a). The goal of organisms is ultimately reproduction, and much work in behavioural ecology rightfully treats them as agents, with fitness providing an ultimate common currency through which to evaluate the importance of different needs of the organisms. However, as Samuelson and Swinkels (2006) rightly argue, organisms cannot just represent their fitness-function to achieve their goal of reproductive success, since the complexity and lack of informational transparency of their situation makes it impossible “to make the agent a *perfect* information processor” (p. 139). Natural selection was constrained in coming up with proximate mechanistic utility functions over actions in a variety of life situations that in many cases will not directly map unto fitness, but nevertheless function in very analogous ways. Edmund Rolls

(1999) made a useful distinction here between the kind of choice mechanisms that are more fixed such as are found in plants, and those choice mechanisms that are sensitive to learning in the achievement of a goal, since nature is typically not transparent and the values of different actions have to be learned - and often *un*learned. While Rolls wasn't concerned with consciousness per se, he maintained that "a common reward-based currency appears to be the fundamental solution that brains use in order to produce appropriate behaviour" (Rolls 1999, p. v), and Dawkins (2001) thinks that this distinction can help us to better make sense of the role of consciousness in choice problems animals face.

What we are interested in here is the evolution of a major transition in agency as a natural phenomenon, rather than as a property of all living systems.¹⁴ To learn about the workings of the internal mechanisms that achieve this end of teleonomic action evaluation, behavioural ecologists readily recognized that we need something like a common currency to compare different actions:

Any attempt to understand behavior in terms of the evolutionary advantage that it might confer has to find a "common currency" (McFarland and Sibly 1975; McCleery 1977) for comparing the costs and benefits of various alternative courses of action.

– McNamara and Houston (1986, p. 358)

I owe much here to the work of the neuroscientist Michel Cabanac who has perhaps been the most prominent contemporary defender of the old utilitarian *Benthamite* idea that animals have a proximate common currency in the form of the hedonic experience of pleasure and pain,¹⁵ which he argues is implicated in the evolution of sentience in the early Amniota. Together with his collaborators, Cabanac has long emphasized the importance of positive and negative feelings in decision-making trade-offs in both humans and non-human animals (Cabanac 1971, 1979; Cabanac and Johnson 1983; Cabanac 1996, 1992; Balasko and Cabanac 1998b,a; Cabanac 1999; Cabanac et al. 2009). This is a different kind of common currency claim from that of McNamara and Houston, which is not about the problem of how behavioural ecologists ought to model economic problems faced by organisms, but rather how organisms themselves deal with their economic trade-offs. Here, the common currency is a real psychological state:

¹⁴ In a review essay on his 2018 monograph on agency as a concept in evolutionary biology, I criticized Okasha for having little to say on the actual evolution of agency as a real phenomenon in nature (Veit 2021e).

¹⁵ See also Leknes and Tracey (2010) for a defense by two prominent affective neuroscientists of Bentham's idea that pleasure and pain are the masters of mankind.

In natural settings, the goals competing for behavior are complex, multidimensional objects and outcomes. Yet, for orderly choice to be possible, the utility of all competing resources must be represented on a single, common dimension.

– Shizgal and Conover (1996, pp. 37-38)

While Shizgal and Conover do not argue that such a common currency must be conscious, one can readily see why Cabanac connects such common currency claims to argue that hedonic valence will be able to function as a mechanistic proxy that mirrors the trade-offs of the fitness-maximization problem of organisms. Such a proximate common currency adds functional value by making the complexity of the computational problem tangible, enabling organisms with high degrees of freedom to weigh alternative courses of action against each other.

Organisms are often faced with what microeconomics studies as a so-called ‘substitution problem’.¹⁶ Some needs and motivations are substitutes, i.e. one can be satisfied (at least partially) by satisfying the other. Others, such as sleep and foraging, conflict and need to be evaluated against each other in terms of importance. Benefits of one action need to be computed against the costs of foregoing another and the difficulty of this pathological complexity is rarely given enough appreciation, as if accurate representations of the world alone could fuel adaptive success. Both Godfrey-Smith and Sterelny in their emphasis on environmental complexity in the evolution of mind have neglected this ‘internal’ source of teleonomic complexity and underestimate the difficulty of achieving efficient action selection (see also Spurrett 2020). This is why the pathological complexity thesis treats the diversity of subjective experiences as something that must ultimately be subservient to evaluation, since it is here that consciousness becomes discharged in action. Like Cabanac, I argue for the Benthamite idea that pleasure and pain are central in the evolution of animal life, though I will argue that the evolutionary origins of this capacity are quite a bit older than he suggests.

3 The Cambrian Explosion in Pathological Complexity

[I]t seems certain, as a matter of observable fact, that the association of Pleasure and Pain with organic states and processes which are respectively beneficial and deleterious to the organism, is the most important function of Consciousness in the scheme of

¹⁶ See Shizgal’s response to the question of whether there is a common currency for all sensory pleasures in Kringelbach and Berridge 2010, p. 18).

Evolution. And for this reason I have placed the origin of Pleasures and Pains very low down in the scale of conscious life.

– George John Romanes (1883, p. 111)

If dealing with pathological complexity is the *raison d'être* of hedonic valence, it leads us to look in the history of life for explosions in complexity that plausibly made this capacity worth having. Doing so makes consciousness no longer just a problem biologists may or may not want to address as an explanandum, but an explanation for a rise in biological complexity itself. The most rapid and puzzling explosion of complexity in the history of life is the Cambrian explosion 541 million years ago. This explosion was central to the evolution of animals, since it is here that we observe the origin of many of the basic metazoan body plans we see today (Maloof et al. 2010). Stephen J. Gould (1996) even argued that it constituted the highest degree of diversity in animal life forms even, making it maximally *disparate*.¹⁷ The label ‘Precambrian’ emphasises the importance placed on divide represented by the Cambrian period; seemingly representing the evolutionary equivalent of the Christian practice of identifying all time prior to the alleged birth of Jesus as ‘BC’.

However, it is contested as to just what caused this explosion of complexity. This lack of a satisfying explanation has led some scientists and philosophers to seriously consider the possibility that we may be able to feed two birds with one scone, by suggesting that subjectivity, agency, and other capacities related to consciousness form a (partial) explanation for the Cambrian explosion (see for instance Trestman 2013; Feinberg and Mallatt 2016; Godfrey-Smith 2016; Ginsburg and Jablonka 2019). If they are right, this would be an early birth of consciousness, indeed. Nevertheless, over the ‘short’ timespan of the next 20 million years the Cambrian explosion led to complex multicellular body plans, nervous systems, behavioural repertoires, and modes of sensing in several different lineages that we now see as the most likely candidates for subjective experience (Trestman 2013).

A New Mode of Being

What we see in the Cambrian is the emergence of a new animal lifestyle in which agency and subjectivity come to play a crucial role: a “different mode of being” (Godfrey-Smith 2020, p. 79).¹⁸ It is these features that come to the mind of most people when they hear the word ‘animal’: active, sensing, and mobile creatures. Indeed, some think that such beings are all sentient. The folk usage of the term ‘animal’ as a reference to living multi-cellular entities capable of goal-directed movement is thus not completely misguided when it is used to refer to something

¹⁷ See Sterelny and Griffiths (1999) for a critical discussion of Gould’s views.

¹⁸ See also Ginsburg and Jablonka (2019).

like a different *mode of being*. Aristotle, who was not aware of the microbial world of life where these capacities can also be found, used the properties of motility, sensing, and goal-directedness to distinguish a special animal mode of being from those of plants, whose mode of being consists in self-maintenance, growth, and reproduction. He called this animal mode of being the ‘sensitive soul’, to be distinguished from the merely ‘nutritive soul’ of plants and the ‘rational soul’ that humans possess in addition to the other two (Aristotle 1991), which influenced Ginsburg and Jablonka (2019) to title their book *The Evolution of the Sensitive Soul*. This way of thinking about animals treats them as possessing something *extra*, rather than a mere reference to a branching in the tree of life. And it is here that I locate the origins of sentience, similarly to Ginsburg and Jablonka (2019) or for that matter Godfrey-Smith’s (2020) *Metazoa*.¹⁹

From an evolutionary perspective, however, the Metazoan branch of life is much older, plausibly branching off from the rest of life 800 million years ago in some more or less recognizable transition towards multicellular individuality.²⁰ During the Ediacaran, which began roughly 635 million years ago and ended with the Cambrian, we find the first definite animal fossils, but they are largely plant-like and their behavioral capacities were simple (Peterson et al. 2008). The ancestors of such lifestyles are, of course, still around us now. Godfrey-Smith (2020) vividly describes how scuba-divers will inevitably encounter something like a ‘breathing forest’ when encountering a ‘garden’ of sponges, corals, and anemones, which are located somewhere between a plant and animal *lifestyle*, yet belong to the animal branch of life.

In the evolutionary scenarios advocated by the aforementioned defenders of an early view of the dawn of consciousness, much focus has been put on interaction *with others*. This makes a lot of sense in a sensory-focused view since it is here that we see the evolution of sophisticated eyes and ‘tools’ such as claws, for the engagement with other organisms. Interaction between *subjects* starts to *matter*; movement can become both ‘flight’ and ‘attack’. In their response to a commentary of mine that introduced the pathological complexity thesis (Veit 2022a), Merker et al. (2022) (mis)interpret pathological complexity as just this emergence of interaction and co-evolutionary arms races in the Cambrian:

Veit proposes that consciousness arose as a means for organisms to deal with what he calls pathological complexity. We assume that what he has in mind is the kind of complexity that arises in coevolution and

¹⁹ I have elsewhere reviewed their work more extensively (see Browning and Veit 2021b; Veit forthcoming).

²⁰ While I have previously written about the challenge of evolving multicellularity (Veit 2019, 2021f), the evolution of multicellular agency constitutes a distinct major transition of its own.

evolutionary arms races, say of the predator–prey kind, which became acute with the evolution of large, imageforming eyes, hence his reference to the Cambrian Explosion.

– Merker et al. (2022, p. 55)

While this new dimension of interaction certainly leads to another explosion in pathological complexity, by making the life-histories of organisms vastly more complex, I don't here locate the very origins of consciousness, but rather the evolution of sensory experience and the origins of other minds thinking (Veit 2021c). As I shall argue, the overemphasis of interaction and sensing is ultimately what distinguishes competing views regarding the evolution of consciousness during the Cambrian from my pathological complexity approach. Taking a look at these competitors will help illuminate this difference.

Ginsburg and Jablonka (2019) see the Cambrian explosion as the driver of what they call *unlimited associative learning* (UAL): a special form of associative learning with a vast openness for new complex behaviour, that they consider a transition marker for the presence of consciousness.²¹ This is because they think that UAL ties together seven widely acknowledged features of consciousness: 1) global accessibility and broadcast, 2) binding/unification and differentiation, 3) selective attention and exclusion, 4) intentionality,²² 5) integration of information over time, 6) an evaluative system, 7) agency and embodiment, and 8) registration of a self/other distinction (Birch et al. 2020, pp. 55-56). The details of this list do not matter much for the goals of this paper and while I readily acknowledge that these features are important for the *shape* of consciousness, like Godfrey-Smith (2021) I am not convinced of the idea that these features all need to appear together for consciousness. The features Ginsburg and Jablonka (2019) derive from various theories of consciousness are based on a model of *human* consciousness, but my goal is explanation of the most minimal kind of subjective experience and I thus find questionable the methodology of looking for shared features of models for the human case.

For evolutionary reasons, we should strongly avoid the idea that we must explain consciousness in terms of a certain rich human form of experience, in which all properties (whatever they are) must be there for an organism to possess subjective experience. The diversity of life should be reflected in very different ways of experiencing the world, so I am skeptical of putting too much emphasis on a certain combination of features, that may instead be arranged in very different ways. The very basis of consciousness is more plausibly found in one of its properties, rather

²¹ See also Birch et al. (2020).

²² In Veit (2022d), I criticize the idea that intentionality and consciousness should be seen as inherently connected. One can be an eliminativist about one and a realist about the other.

than the combination of a variety of capacities that have transformed consciousness across evolutionary time. For this, I emphasize what they list as their sixth hallmark: an evaluative system. The evaluative ability, to avoid harmful stimuli and seek out beneficial ones, is supremely important: survival matters. And some basic capacity for a plus or minus ‘feel’ can readily play an important adaptive role prior to any combining of the above-mentioned ‘hallmarks’.

Others, such as Feinberg and Mallatt (2016), also offer an account of the origins of consciousness in the Cambrian, though their emphasis is on the evolution of eyes and exteroceptive consciousness as the original source of consciousness, which makes sense if one locates the origins of consciousness in the sensory dimensions. However, these approaches have so far failed - as Merker et al. (2022) rightly note in response to the pathological complexity thesis - to address the challenge of why “conscious vision, rather than simply better visually based performance operating unconsciously, is needed to meet the transition’s functional challenge” (p. 55). The correct response here is of course that the origins of consciousness lie in the functional role of dealing with the complex trade-offs arising from the earlier explosion in pathological complexity due to the demands of controlling a multicellular animal body.

Lastly, Godfrey-Smith primarily emphasizes agency and subjectivity, but these do not constitute a single property. They constitute a variety of capacities that can be described as making organisms more agent-or-subject-like in some respects. While a detailed evolutionary journey from more object-like organisms to genuine conscious subjects will inevitably involve the gradual evolution of subjective experience and make consciousness less mysterious, it tells us little about the *raison d’être* and very origins of consciousness, unless we investigate the evolutionary origins of capacities that make organisms more subject-like.

While I think that all of the above approaches are important for understanding the evolution of consciousness, my problem with all these hypotheses is that they already assume some basic capacity for action and sensing as a given, which they then argue leads to interaction driving an arms-race in which subjective experience makes sense. But in all this focus on *interaction*, it is lost that action itself constitutes a major problem (as the work by Keijzer and colleagues nicely demonstrates). And I contend that it is the solution to this problem that caused the Cambrian explosion.

Action!

Some clarificatory remarks on my usage of the term ‘action’ will be useful here, since it is in the evolution of action that pathological complexity explodes and evaluative experience arises. Following Spurrett (2020) and the ethologists, I treat ‘action’ here in the teleonomic sense of any kind of functional activity produced by biological

agents in their usage of their degrees of freedom, rather than (as is common in much of philosophy of mind and action) as an exclusive term for intentional behaviour.²³

This view is deliberately broad, to include minimal senses of action such as that of plants producing chemical defenses, and is closer to work in robotics, artificial intelligence, and cybernetics where the computational complexity of building a teleonomic system is readily recognized. This broader notion will help us to better think about a major transition of action and agency in the animal branch of life. The expansion of the organismal optionspace - or as a cyberneticist might describe it: an organism's degrees of freedom - are what cause a computational explosion in pathological complexity for modeller and organism alike.

Action, of course, was not invented by animals. Evaluations are found even in single-celled bacteria who swim, sense, hunt, and make decisions in the broad teleonomic sense of action I employ here. Pathological complexity is a property of all life and is not restricted to animals. Yet, I do not follow the biopsychist path of using evidence for evaluations in bacteria as evidence for consciousness. Such thinking seems motivated once again by a resistance to evolutionary thinking about consciousness as something that gradually 'emerges'. In Godfrey-Smith's *Metazoa*, there is a notable shift towards taking the challenge by Keijzer more seriously. Here, he describes action as having to be reinvented at a larger scale with new forms of coordination (2020, p.53). When evolution has to reinvent or discover something at a new level of biological organization things can take a very different shape and become vastly more complex. Multicellular action "involves coordination across vast scales from a cell's point of view" (Godfrey-Smith 2020, p.53). The challenge of organizing a multi-cellular unit is vastly more difficult than the challenge of organizing a single cell. But once this challenge has been mastered, a vast possibility space for new ways of life has been opened.

Here, I should reply to the same kind of question that Godfrey-Smith responds to when he asks why we should emphasize actions of movement over the production of chemicals or other basic activities of life. He argues that controlled motion was a new landmark in innovation, a major transition of action, that made organisms objects of a new kind (Godfrey-Smith 2020, p. 55). We can make this more precise by defining this kind of transition as the control of an organism's degrees of freedom in the service of a functional end, e.g. feeding or moving in one direction over another. Rather than multiple actions at the same time, this major transition of agency allows for wholebody actions to the exclusion of others, and thus leading to the evolution of choice. The origins of this invention in the animal tree of life can be seen in the ancestors of modern *Alyonacea*, or soft corals, who largely stuck with *minimal action* in the form of a grasping behaviour. it is here that we find a boundary-case to think about the evolution of hedonic valence.

²³ This parallels the use of 'behaviour' as functional activity by Millikan (1995).

The biological world has few hard boundaries and we see something of a gradual transition in nervous systems from playing the role of internal organization to taking a more outward-oriented role, such that action slowly emerges out of development (Godfrey-Smith 2002). This is why Spurrett (2020) notes that some activities of plants do constitute genuine behaviour, e.g. in a Venus flytrap (p. 7). But in a gradualist picture from discriminating development towards active agency, it would be a mistake to follow the move of some plant scientists such as Monica Gagliano (2017, 2018) and fail to recognize that a major transition in agency took place in the evolution of a distinctively recognizable animal lifestyle.

We can readily acknowledge the force of the argument that the striking cognitive and behavioral capacities of plants, or for that matter bacteria, have been given too little attention, but the right move here is to strongly endorse a previously neglected evolutionary gradualism, rather than deny important gradations in agency. Unfortunately, the cognitive sciences have shown at least a partial blindness towards such evolutionary considerations.²⁴ We should simply not think about agency as an all-or-nothing affair, a mistake that has also led to an overreaching at the other side of the spectrum, where the presence of agency in all of life is identified with sentience (e.g. Reber 2016).

As the work of Keijzer emphasizes, two important innovations that largely came together in the transition to a distinctive kind of animal agency are the nervous system and muscles that tied animal bodies together in new ways and allowed for a new set of adaptive capacities to be built on top. Since subjective experience is often closely associated with the nervous system, it is useful to think about the very origins of nerves and neurons. Here, the role of muscles has been underestimated, with nerve-nets largely playing the role of controlling muscles in the service of adaptive behaviour. In such a picture it makes sense for a rapid explosion of innovation to occur - in the form of sensory organs and tools such as claws to engage with other organisms but the actual explosion in complexity, I argue, was enabled by a transition in the organization of action-selection. It is here that we find the dawn of subjectivity prior to the dimensions of sensory experience and selfhood.

The Dawn of Consciousness Explained

To demonstrate the significance and difficulty of this major transition towards a distinctive kind of animal agency one has to look no further than the timespan it took from the origins of animal life to a distinctive animal lifestyle. The first definite animal fossils date back to the late Ediacaran, though it has been contested whether to even call them animals, with their odd flower-like shapes, occurring long before the evolution of plants. *Dickinsonia*, which has been one of the paradigm animals of the

²⁴ A point I have also made elsewhere (Veit and Browning forthcomingc,f).

Ediacaran, does not appear to have eyes or appendages that could give rise to interesting new ways of sensory-motor couplings. Godfrey-Smith (2020) describes the biological imagination of this puzzling period as quiet and placid, with no evidence for interaction: “There are almost no signs of predation—no half-eaten individuals, no sign of the built-in weapons, offensive and defensive, that animals tend to have now” (p. 64). More importantly, however, is the striking absence of action in Spurrett’s (2020) sense of degrees of freedom with alternative uses. Genuine action selection does not appear until much later.

Some change to this action-less picture began in the late Ediacaran 575 million years ago, until the beginning of the Cambrian, with discernable transition taking place in animals. Waggoner (2003) distinguished three periods: Avalon, White Sea, and Nama. Strictly speaking, these three names were used to denote three major ‘assemblages’, i.e. findings of a collection of species that fossilized around the same time. But despite new data coming in, the paleontological picture of three distinct periods has largely remained. The first of these periods is the most important, since it is here that recent discussion in the field have placed a possible earlier explosion in animal complexity. Following comprehensive quantitative data analysis of the fossil evidence, Shen et al. (2008) argued that there was an ‘Avalon Explosion’ in the Ediacaran morphospace, mirroring the Cambrian explosion. Here, it is useful to ask for possible mechanistic explanations as to why one explosion failed, whereas the other succeeded. While the White Sea showed definite signs of bilaterian bodies and more discernible actions of crawling on the seafloor, the Nama largely sees the disappearance of these larger complex and mobile animals, before they returned with a vengeance during the Cambrian.

Why such animal lifestyles failed despite gradual increases in sensory-motor capacities has puzzled Godfrey-Smith (2020), who seeks to ground consciousness in the gradual evolution of just such capacities. Shen et al. (2008) ask but do not answer the question of what “constrained the Ediacara morphospace from further expansion or shift in the subsequent White Sea and Nama assemblages?” (p. 84). Here, the pathological complexity thesis offers us an elegant explanation for why one explosion failed, whereas the other succeeded. The answer is the necessity of an evaluating system, which enables the efficient deployment of the increase in behavioral complexity through the gradual increase in sensory-motor capacities. Whereas organisms in the White Sea failed to deal with the computational explosion of pathological complexity caused by the rapid expansion of their degrees of freedom, the Cambrian saw the evolution of *Benthamite* creatures with a common currency of hedonic valence for efficient action-selection.

Here, the status of my concept of pathological complexity as *the* explication of the teleonomic complexity of organisms becomes important once again. The complexity that matters for the organism is first and foremost a problem to be solved, not an adaptation in itself. The real problem that was solved during the Cambrian,

but not the Avalon explosion, was an efficient way of dealing with the complexity increase of action-selection. Since natural selection can only act upon behavior by modifying the architecture behind decision-making mechanisms, McNamara and Houston (2009) argued that we need to combine the mechanistic research of physiologists with the adaptationist research of evolutionary biologists into an integrated study of function and mechanism.

In the mathematical framework of state-based behavioural and life history theory it is obvious that an increase in variables will lead to a computational explosion in complexity in attempting to find the best strategies. How can organisms solve this? The problem has been given far too little attention, despite the fact that more agential organisms have to solve a problem themselves that natural selection usually solves 'for' life, i.e. how to engage in the *right* fitness-enhancing activities. For much of life these are a given, but for animals with high degrees of freedom, there is a constant need to compare the returns and costs of various actions, opportunities, and dangers associated with both internal and external changes. The reason that I suspect the Avalon explosion 'failed' is because these organisms did not come up with a design solution to pay off this complex investment into behavioral flexibility. They did not have a common currency of valence to make this complexity manageable in a bottleneck that resembles that of natural selection both for propagules and species.

As Charles Sherrington (1906) argued early on in his work on the goal-directedness of the nervous system, organisms require some form of informational bottlenecking - what he called a *final common path* - in order to deal with the problem of coordinating competing actions. Now, it is probably too much to demand that everything we've called 'action' goes through a single mental bottleneck - that kind of thinking takes us back to an older Cartesian materialist model of the mind with a homunculus and a Cartesian theater that Dennett sought to dispel. But Spurrett (2020) is right to insist that there is something of an intermediate position here, "a useful corrective to the tradition [...] that regards almost any convergence in a control system as a symptom of allegiance to muddled models of intelligence and cognition" (p. 11). Spurrett is referring here to the likes of Brooks (1991) who argued that representational higher-order processing for actions would lead to significant bottlenecks with delays or even paralysis and that in this case the world itself can serve as its own best representation (see also Clark 1997).

Some bottlenecking is required for an animal lifestyle, since information about both internal and external states is at least to some extent opaque, and the execution of one action over another requires the combination of a variety of capacities that, as Spurrett (2020) rightly notes, itself includes trade-offs "between other possible allocations of individual capacities and combinations of them, over and above whatever the metabolic and other direct costs of this or that action might be" (p. 11). But unfortunately little attention has been given to this increase in complexity as a problem that has to be dealt with. Action production is taken for granted in debates

on the evolution of consciousness, even in the Cambrian, in the work of Ginsburg and Jablonka, Godfrey-Smith, Feinberg and Mallatt, but it cannot be disassociated from action selection. In dealing with this complexity, organismal decisions will be made, or rather filtered/narrowed, for computational reasons through a number of different sub-agencies, but much work in neuroeconomics strongly supports the idea that there is in fact something like a global common currency for a huge variety of choice types, if not all (Spurrett 2020).²⁵

It is thus not surprising that Shizgal and Conover (1996) maintained that orderly choice is indicative that there must be some form of value ranking on a common scale - this argument is routinely made by revealed preference theorists in economics. Valence plausibly constitutes an ancient solution to this problem in the Cambrian, which then enabled the evolution of richer kinds of felt sensory representations like Denton's (2006) primordial emotions, such as thirst and hunger, directly tied to an evaluative system of efficient decision-making. An evolutionary perspective turns on its head the common view that hedonic valence is something that came on top of sensory consciousness, by making subjective (expected) utility its most ancient capacity. The pathological complexity does therefore not just imply a metaphorical sense of the existence of a common currency, but a psychologically real *felt* common currency. And it is because of this that my account offers an elegant answer to the challenge of why some sensory processes are felt and others aren't.

Unfortunately, comparative neuroeconomics remains an incredibly small field, with much of its research focused on standard model organisms such as monkeys, rodents, and birds. But what little research has been done strongly supports the idea that analogues to the human final common path are found throughout a wide range of the animal branch of life. This is precisely where we'd expect to see the presence of a common currency, in the form of specialized neural circuits designed for the exclusion of mechanically incompatible actions that can compete against each other in a preference ordering, and also, as Spurrett (2020) emphasizes, "the last place [preferences] can do so" (p. 22). It is now clear that almost all vertebrates share an evaluative neural system for reward and 'punishment' with dopamine and other valence-related molecules sharing a deep evolutionary origin that is plausibly very ancient, rather than invented multiple times.

The observation that some species taken to lack sentience, such as nematodes, use dopamine (alongside other such molecules implied in valence) to organize action and motor activity (see Barron et al. 2010) is only further evidence of an ancient origin of valence to help organisms achieve efficient action selection. As Spurrett (2020) notes, it is highly likely that the first implementations of preferences "were

²⁵ See Levy and Glimcher (2012, 2016); Pearson et al. (2014) for excellent reviews of the neuroeconomics literature.

elaborations of motor control systems shared with creatures that couldn't learn, but could move" (p. 23). Indeed, it does appear that dopamine is at least as old - if not older - as the invention of the bilaterian body plan with symmetric halves that enabled a vast increase in possibility for animal action (Caveney et al. 2006). In the theory defended here we might thus see a valence system as the revolution needed to make animal agency 'pay off', providing an efficient action selection mechanism as the final behavioural common path of metazoans for the prioritization of some actions over others in the complexity increase of more degrees of freedom.²⁶ What evidence has been gathered in invertebrates is highly suggestive that this is not a unique vertebrate trait (Gibbons et al. 2022). If not for the standard methodological practice in comparative cognition to only attribute these capacities to animals in which these capacities have been demonstrated, the capacities would already be seen as much more basic. We're here unfortunately faced by something of a methodological artefact, by the sad observation that studies of motivational trade-offs - such as those of Cabanac and Elwood - have until recently been very rare in animals distantly related to us.

Unlike Spurrett, who tries to bracket off consciousness and emotions in his work on the origins of preferences as representational capacities, I view them as being initially instantiated through a hedonic valence system that later becomes more representational through acquiring richer sensory and integrative capacities. The evolutionary ancestors of preferences are not instantiated in the cognitive or representationalist sense of a calculation, but rather an instantaneous general feeling of one's state - a total state of momentary *feeling* in just that sense of the word.²⁷ Such a model of the origins of hedonic feels makes it immune to the challenge of Lloyd Morgan's canon, as it is something substantially simpler than representationalist valuerankings. Dennett (1995) once called organisms capable of reinforcement learning *Skinnerian creatures*, but a better term less reliant on externalist modes of thinking about what happened in the transition to animal agency would be *Benthamite creatures*.

Capacities for reinforcement learning are highly suggestive of preferences, implying "both sensitivity to rewards and updating behavioural dispositions in light of reward-based consequences of earlier behaviour" (Spurrett 2020, p. 23). It is thus hardly surprising that earlier evolutionists took the presence of such learning abilities as almost certain evidence that these animals feel pleasure and pain. But because of the apparent ubiquity of this ability in the animal branch of life, in cephalopods,

²⁶ See also Brunet and Arendt (2016); Arendt et al. (2016).

²⁷ While economists have struggled to quantitatively measure such hedonic utility, this does not imply that it doesn't exist or that psychological utilitarianism must be abandoned (Browning and Veit 2021a).

crustaceans, and insects (Perry et al. 2013)²⁸, many have come to endorse the view that this would make consciousness too simple, that it requires something more. This conclusion was wrong in two ways: firstly, a gradualist evolutionary perspective of the evolution of consciousness ought precisely to endorse a very humble origin for the origin of sentience, and secondly, the ability for reinforcement learning is far more complex than is typically acknowledged, with cyberneticists struggling to design robots achieving even the most basic successes of simple animal life. No robot has yet been created that would be able to handle the pathological complexity of the life histories exhibited in even the most basic distinctively animal lifestyles. Their failure is akin to the very same challenge Avalonian and White Sea animal agents failed to overcome.

What we find at the verge of the Cambrian explosion is the evolution of subjective utility maximizers upon which more complex representational capacities such as interoception and emotions were built. Here, I am not implying that all new capacities must go through the bottleneck of the evaluative system and be consciously experienced. But it is within the context of such evaluative agency that subjective experience *makes sense*, and plays a distinctive role in the sense of functional deployment of the degrees of freedom a flexible animal lifestyle offers. This approach substantially narrows the explanatory gap and makes subjective experience something almost necessary for organisms to undergo a major transition from ‘mere’ objects subject to the whims of external forces into genuine agents/subjects in their own right, and thus makes great progress in the completion of the Darwinian revolution

4 Conclusion and Further Objections

The goal of this article was to advance a new hypothesis about the origins of consciousness, which was in turn motivated by the ethologists’ demand to pay close attention to organisms as teleonomic agents with life-history strategies in their natural environments. Without an understanding of what these organisms evolved *to do* it will be impossible to distinguish the normal from the pathological - including their subjective experience. From an evolutionary point of view, health has to be understood as a measure of how an organism deals with the pathological complexity it is faced with: it is the *ultimate* teleonomic measure of organismal complexity. And pathological complexity can be operationalized as the complexity of the number of parameters and constraints in the optimization problem studied by state-dependent or statebased behavioural and life history theory. With the evolution of behavioural flexibility, the Cambrian explosion brought forth an explosion in pathological

²⁸ Note that all these animal groups are now slowly entering the accepted realm of animals with sentience.

complexity of how to control and select the right action at the right time - a problem that I argued was dealt with through the evolution of a proximate common currency of hedonic valence.

By using the pathological complexity framework to think about the life-history challenges of different organisms, we are placed in a better position to make predictions regarding their subjective experiences, which can then be used in a feedback process to better understand their pathological complexity, thus ultimately allowing us to create an evolutionary framework for the study of animal consciousness. In a compendium article to this paper, I draw on life history research in insects to investigate whether claims regarding the possibility of pain in ants, bees, flies and the like makes sense in the context of their robotic, short, and fast lives (Veit 2022e). By paying close attention to the life histories of animals such as bees, who routinely engage in difficult economic trade-offs, I argue that it will no longer appear as dubious to attribute sentience to them. In regards to sensory experiences, we will similarly be able to make predictions about the discrimination capacities of animals such as birds by studying what the evolutionarily salient features of their environments consist in. What my framework provides is a pathway towards a cognitive ethology, as Griffin (1976) once intended, that can make sense of the subjective experiences of animals by asking what role it may play for them in their normal healthy lives. As I've recently argued, the "future of animal sentience research lies not in drawing boundaries but in empirically investigating *what it feels like to be* an echo-locating bat, an infrared-sensing snake, an octopus with multiple distributed ganglia, a fish without a neocortex, or an arthropod such as a spider or a honey bee" (Veit and Huebner 2020, p. 3).²⁹

Beyond science, the pathological complexity thesis may also help us in ethics and policy-making, since it is sentience that is usually taken to make an entity a subject of moral concern (Sebo 2018; Browning 2020c). Browning (2020b) has even defended a Benthamite view of animal welfare by drawing on the idea of a common currency for evaluation. As my interest in animal consciousness was also motivated by ethical concerns, I have published several papers on animal ethics, sentience, and welfare science in collaboration with Browning,³⁰ but one problem we were repeatedly faced with is the challenge of inter-species comparisons of welfare (see Browning 2022b for a detailed examination). The more broadly we attribute sentience to other animals, the less reasonable it will be to assign equal moral weight to all insects, birds, and octopuses. Their capacity to suffer and experience pleasure reasonably scales according to their degree of consciousness, which should force us

²⁹ A book-length treatment of the pathological complexity thesis will be offered elsewhere (see Veit 2022c).

³⁰ See Veit and Browning (2020a,a, 2021b); Browning and Veit (2020b,a, 2021c, 2022, forthcoming).

to think about their consciousness as well as their ethical status in a gradualist manner. While we have offered some brief discussions on animal sentience in relation to the life histories of different animals (Browning and Veit 2021d), the pathological complexity thesis may offer us a useful evolutionary proxy measure to assess different levels of evaluative richness in the subjective experience of different animals. How to measure animal welfare is a notoriously difficult problem (Dawkins 1980; Browning 2022a), but a measure of pathological complexity would enable us to rank animals according to a so-called *sentience multiplier* (see Browning 2020a). But to make use of the pathological complexity for this purpose will be a task for future work.

Lastly, while the available evidence cannot rule out many competing theories of consciousness just yet, my thesis has two major points in its favour that advantage it against many contenders in the field. Firstly, the ‘hard problem’ of why things feel a certain way, does not appear to be as much of a challenge within a hedonic framework. Things feel a certain way, because they *have to* feel that way to be functional. This is the first major advantage: overcoming the alleged inability of functionalist theories of consciousness to explain why consciousness *feels* like anything at all. Secondly, the pathological complexity thesis allows us to make predictions regarding the subjective experiences of other animals. This is a second major advantage against most competitors that have a hard time making testable predictions that could refine our theoretical framework. While the specific thesis advocated here may turn out to be wrong, the integration of ecological and evolutionary thinking into a science that has suffered from a human-centric bias will allow us to develop a firm mid-level theory not contingent upon the human case, and thus help us to transition towards a true biological bottom-up study of consciousness that tries to answer the teleonomic question of what it is *for*.

References

- Arendt, D., M. A. Tosches, and H. Marlow (2016). From nerve net to nerve ring, nerve cord and brain—evolution of the nervous system. *Nature Reviews Neuroscience* 17(1), 61.
- Aristotle (1991). *On the Soul* (J. Barnes, Ed., J. A. Smith, Trans.). *The Complete Works of Aristotle: The Revised Oxford Translation, vol. 1*. Princeton, NJ: Princeton University Press.
- Balasko, M. and M. Cabanac (1998a). Behavior of juvenile lizards (*Iguana iguana*) in a conflict between temperature regulation and palatable food. *Brain, Behavior and Evolution* 52(6), 257–262.
- Balasko, M. and M. Cabanac (1998b). Motivational conflict among water need, palatability, and cold discomfort in rats. *Physiology & behavior* 65(1), 35–41.
- Barron, A. B., E. Søvik, and J. L. Cornish (2010). The roles of dopamine and related compounds in reward-seeking behavior across animal phyla. *Frontiers in behavioral neuroscience* 4, 163.

- Birch, J., D. M. Broom, H. Browning, A. Crump, S. Ginsburg, M. Halina, D. Harrison, E. Jablonka, A. Y. Lee, F. Kammerer, et al. (2022). How Should We Study Animal Consciousness Scientifically? *Journal of Consciousness Studies* 29(3-4), 8–28.
- Birch, J., C. Burn, A. Schnell, H. Browning, and A. Crump (2021). Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans. *LSE Consulting*.
- Birch, J., S. Ginsburg, and E. Jablonka (2020). Unlimited Associative Learning and the origins of consciousness: a primer and some predictions. *Biology & philosophy* 35(6), 1–23.
- Bonner, J. T. (1988). *The Evolution of Complexity*. Princeton: Princeton University Press.
- Brooks, R. A. (1991). Intelligence without Representation. *Artificial intelligence* 47, 139–159.
- Browning, H. (2020a). Assessing Measures of Animal Welfare. *Preprint*. <http://philsci-archive.pitt.edu/17144/>
- Browning, H. (2020b). *If I Could Talk to the Animals: Measuring Subjective Animal Welfare*. Ph.D. thesis, Australian National University. <https://doi.org/10.25911/5f1572fb1b5be>
- Browning, H. (2020c). The natural behavior debate: Two conceptions of animal welfare. *Journal of Applied Animal Welfare Science*, 325–337. <https://doi.org/10.1080/10888705.2019.1672552>.
- Browning, H. (2022a). The Measurability of Subjective Animal Welfare. *Journal of Consciousness Studies* 29(3-4), 150–179.
- Browning, H. (2022b). The problem of interspecies welfare comparisons. *Preprint*.
- Browning, H. and J. Birch (2022). Animal sentience. *Philosophy Compass*, e12822.
- Browning, H. and W. Veit (2020a). Confined Freedom and Free Confinement: The Ethics of Captivity in *Life of Pi*. In Á. T. Bogár and R. S. Szigethy (Eds.), *Critical Insights: Life of Pi*, pp. 119–134. Salem Press.
- Browning, H. and W. Veit (2020b). Is Humane Slaughter Possible? *Animals* 10(5), 799.
- Browning, H. and W. Veit (2021a). Does utilitarianism need a rethink? Review of Louis Narens and Brian Skyrms' *The Pursuit of Happiness*. *Journal of Economic Methodology*, 1–5.
- Browning, H. and W. Veit (2021b). Evolutionary biology meets consciousness: essay review of Simona Ginsburg and Eva Jablonka's *The Evolution of the Sensitive Soul*. *Biology & Philosophy* 36(5), 1–11.
- Browning, H. and W. Veit (2021c). Freedom and animal welfare. *Animals* 11(4), 1148.
- Browning, H. and W. Veit (2021d). Positive Wild Animal Welfare. *Preprint*.
- Browning, H. and W. Veit (2022). The importance of end-of-life welfare. *Animal Frontiers* 12(1), 8–15.
- Browning, H. and W. Veit (forthcoming). More than Zombies: Considering the Animal Subject in De-Extinction. *Ethics, Policy & Environment*.
- Brunet, T. and D. Arendt (2016). From damage response to action potentials: early evolution of neural and contractile modules in stem eukaryotes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1685), 20150043.
- Cabanac, M. (1971, September). Physiological role of pleasure. *Science* 173(4002), 1103–1107.
- Cabanac, M. (1979, March). Sensory pleasure. *The Quarterly Review of Biology* 54(1), 1–29.
- Cabanac, M. (1992). Pleasure: the common currency. *Journal of Theoretical Biology* 155(2), 173–200.

- Cabanac, M. (1996). On the origin of consciousness, a postulate and its corollary. *Neuroscience & Biobehavioral Reviews* 20(1), 33–40.
- Cabanac, M. (1999). Emotion and phylogeny. *Journal of Consciousness Studies* 6(6-7), 176–190.
- Cabanac, M., A. J. Cabanac, and A. Parent (2009). The emergence of consciousness in phylogeny. *Behavioural brain research* 198(2), 267–272.
- Cabanac, M. and K. Johnson (1983). Analysis of a conflict between palatability and cold exposure in rats. *Physiology & behavior* 31(2), 249–253.
- Caveney, S., W. Cladman, L. Verellen, and C. Donly (2006). Ancestry of neuronal monoamine transporters in the Metazoa. *Journal of Experimental Biology* 209(24), 4858–4868.
- Clark, A. (1997). *Being there*. MIT Press Cambridge, MA.
- Dawkins, M. (2001). Who Needs Consciousness? *Animal Welfare* 10(1), 19–29.
- Dawkins, M. S. (1980). *Animal Suffering: The Science of Animal Welfare*. London: Chapman and Hall.
- Dawkins, M. S. (1998). Evolution and animal welfare. *The Quarterly Review of Biology* 73(3), 305–328.
- Dennett, D. C. (1995). *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. New York: Simon and Schuster.
- Dennett, D. C. (2017). Suffering matters. *Talk at NYU 2017 Animal Consciousness Conference*.
- Dennett, D. C. (2018). Facing up to the hard question of consciousness. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373(1755), 20170342.
- Denton, D. (2006). *The Primordial Emotions: The Dawning of Consciousness*. Oxford University Press.
- Feinberg, T. and J. Mallatt (2016). *The Ancient Origins of Consciousness*. Cambridge, MA: MIT press.
- Fiorito, G., A. Affuso, D. B. Anderson, J. Basil, L. Bonnaud, G. Botta, A. Cole, L. D'Angelo, P. De Girolamo, N. Dennison, et al. (2014). Cephalopods in neuroscience: regulations, research and the 3Rs. *Invertebrate Neuroscience* 14(1), 13–36.
- Gagliano, M. (2017). The mind of plants: thinking the unthinkable. *Communicative & integrative biology* 10(2), 38427.
- Gagliano, M. (2018). Inside the vegetal mind: on the cognitive abilities of plants. In *Memory and Learning in Plants*, pp. 215–220. Springer.
- Gibbons, M., E. Versace, A. Crump, B. Baran, and L. Chittka (2022). Motivational trade-offs in bumblebees. *bioRxiv*.
- Ginsburg, S. and E. Jablonka (2019). *The Evolution of the Sensitive Soul: Learning and the Origins of Consciousness*. Cambridge: MIT Press.
- Godfrey-Smith, P. (1996a). *Complexity and the Function of Mind in Nature*. Cambridge University Press.
- Godfrey-Smith, P. (1996b, March). Précis of Complexity and the Function of Mind in Nature. *Adaptive Behavior* 4(3-4), 453–465.
- Godfrey-Smith, P. (1996c). Replies to Four Critics. *Adaptive Behavior* 4(3-4), 486–493.
- Godfrey-Smith, P. (1997). Author's response. *Metascience* 6(2), 31–37.
- Godfrey-Smith, P. (2002). Environmental Complexity and the Evolution of Cognition. In R. Sternberg and J. Kaufman (Eds.), *The Evolution of Intelligence*, pp. 223–249. Mahwah, NJ: Lawrence Erlbaum.

- Godfrey-Smith, P. (2016). Animal evolution and the origins of experience. In D. Livingstone Smith (Ed.), *How Biology Shapes Philosophy: New Foundations for Naturalism*, pp. 51–71.
- Godfrey-Smith, P. (2017). Complexity revisited. *Biology & Philosophy* 32(3), 467–479.
- Godfrey-Smith, P. (2020). *Metazoa: Animal Minds and the Birth of Consciousness*. Harper Collins UK.
- Godfrey-Smith, P. (2021). Learning and the biology of consciousness: a commentary on Birch, Ginsburg, and Jablonka. *Biology & Philosophy* 36(5), 1–4.
- Gould, S. J. (1996). In the Mind of the Beholder. In *Dinosaur in a Haystack*, pp. 93–107. London: Jonathan Cape.
- Griffin, D. R. (1976). *The Question of Animal Awareness: Evolutionary Continuity of Mental Experience*. New York: Rockefeller University Press.
- Holland, N. D. (2003). Early central nervous system evolution: an era of skin brains? *Nature Reviews Neuroscience* 4(8), 617–627.
- Keijzer, F. (2015). Moving and sensing without input and output: early nervous systems and the origins of the animal sensorimotor organization. *Biology & Philosophy* 30(3), 311–331.
- Keijzer, F. and A. Arnellos (2017). The animal sensorimotor organization: a challenge for the environmental complexity thesis. *Biology & philosophy* 32(3), 421–441.
- Keijzer, F., M. Van Duijn, and P. Lyon (2013). What nervous systems do: early evolution, input–output, and the skin brain thesis. *Adaptive Behavior* 21(2), 67–85.
- Kringelbach, M. and K. Berridge (2010). *Pleasures of the Brain*. Oxford: Oxford University Press.
- Leknes, S. and I. Tracey (2010). Pain and pleasure: masters of mankind. In M. Kringelbach and K. Berridge (Eds.), *Pleasures of the Brain*, pp. 320–336. Oxford: Oxford University Press.
- Levy, D. and P. Glimcher (2016). Common value representation—A neuroeconomics perspective. *Handbook of value: Perspective from economics, neuroscience, philosophy, psychology and sociology*, 85–118.
- Levy, D. J. and P. W. Glimcher (2012). The root of all value: a neural common currency for choice. *Current opinion in neurobiology* 22(6), 1027–1038.
- Maloof, A. C., S. M. Porter, J. L. Moore, F. Ö. Dudás, S. A. Bowring, J. A. Higgins, D. A. Fike, and M. P. Eddy (2010). The earliest Cambrian record of animals and ocean geochemical change. *GSA bulletin* 122(11-12), 1731–1774.
- Mangel, M. and C. W. Clark (1986). Towards a unified foraging theory. *Ecology* 67(5), 1127–1138.
- McCleery, R. (1977). On satiation curves. *Animal Behaviour* 25, 1005–1015. McFarland, D. and R. Sibly (1975). The behavioural final common path. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 270(907), 265–293.
- McNamara, J. M. and A. I. Houston (1986). The common currency for behavioral decisions. *The American Naturalist* 127(3), 358–378.
- McNamara, J. M. and A. I. Houston (2009). Integrating function and mechanism. *Trends in ecology & evolution* 24(12), 670–675.
- Merker, B., K. Williford, and D. Rudrauf (2022). The integrated information theory of consciousness: Unmasked and identified. *Behavioral and Brain Sciences* 45.
- Millikan, R. G. (1995). *White queen psychology and other essays for Alice*. MIT Press.

- Nesse, R. M. and G. C. Williams (1995). *Evolution and Healing: The New Science of Darwinian Medicine*. London: Weidenfeld & Nicolson.
- New England Anti-Vivisection Society, American Anti-Vivisection Society, The Physicians Committee for Responsible Medicine, The Humane Society of the United States, Humane Society Legislative Fund, J. Jacquet, B. Franks, J. Pungor, J. Mather, P. Godfrey-Smith, L. Marino, G. Barord, C. Safina, H. Browning, and W. Veit (2020). Petition to Include Cephalopods as “Animals” Deserving of Humane Treatment under the Public Health Service Policy on Humane Care and Use of Laboratory Animals. *Harvard Law School Animal Law & Policy Clinic*, 1–30. <https://doi.org/10.13140/RG.2.2.27522.30401>
- Okasha, S. (2018). *Agents and goals in evolution*. Oxford University Press.
- Pearson, J. M., K. K. Watson, and M. L. Platt (2014). Decision Making: the Neuroethological Turn. *Neuron* 82(5), 950–965.
- Perry, C. J., A. B. Barron, and K. Cheng (2013). Invertebrate learning and cognition: relating phenomena to neural substrate. *Wiley Interdisciplinary Reviews: Cognitive Science* 4(5), 561–582.
- Peterson, K. J., J. A. Cotton, J. G. Gehling, and D. Pisani (2008). The Ediacaran emergence of bilaterians: congruence between the genetic and the geological fossil records. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363(1496), 1435–1443.
- Pittendrigh, C. S. (1958). Adaptation, natural selection, and behavior. In A. Roe and G. G. Simpson (Ed.) *Behavior and Evolution*. New Haven: Yale University Press
- Reber, A. S. (2016). Caterpillars, consciousness and the origins of mind. *Animal Sentience: An Interdisciplinary Journal on Animal Feeling* 11(1).
- Rolls, E. T. (1999). *The Brain and Emotion*. Oxford: Oxford University Press.
- Romanes, G. J. (1883). *Mental Evolution in Animals, with a Posthumous Essay on Instinct by Charles Darwin*. London: Kegan Paul, Trench.
- Samuelson, L. and J. M. Swinkels (2006). Information, evolution and utility. *Theoretical Economics* 1(1), 119–142.
- Schnell, A., H. Browning, and J. Birch (2022). Octopus farms raise huge animal welfare concerns - and they're unsustainable too. *The Conversation*. <https://theconversation.com/octopus-farms-raise-huge-animalwelfare-concerns-and-theyre-unsustainable-too-179134>.
- Sebo, J. (2018). The moral problem of other minds. *The Harvard Review of Philosophy* 25, 51–70.
- Shen, B., L. Dong, S. Xiao, and M. Kowalewski (2008). The Avalon explosion: evolution of Ediacara morphospace. *Science* 319(5859), 81–84.
- Sherrington, C. S. (1906). *The Integrative Action of the Nervous System*. New Haven, CT: Yale University Press.
- Shizgal, P. and K. Conover (1996). On the neural computation of utility. *Current Directions in Psychological Science* 5(2), 37–43.
- Spurrett, D. (2015). The natural history of desire. *South African Journal of Philosophy* 34(3), 304–313.
- Spurrett, D. (2020). The descent of preferences. *The British Journal for the Philosophy of Science*.
- Sterelny, K. (1997). Where Does Thinking Come From? A Commentary on Peter Godfrey-Smith’s Complexity and the Function of Mind In Nature.

- Biology and Philosophy* 12(4), 551–566.
- Sterelny, K. (2003). *Thought in a Hostile World*. Oxford: Blackwell.
- Sterelny, K. and P. E. Griffiths (1999). *Sex and death: An introduction to philosophy of biology*. University of Chicago press.
- Trestman, M. (2013). The Cambrian explosion and the origins of embodied cognition. *Biological Theory* 8(1), 80–92.
- Veit, W. (2019). Evolution of multicellularity: cheating done right. *Biology & Philosophy* 34(3), 34.
- Veit, W. (2021a). Agential thinking. *Synthese*, 1–27.
- Veit, W. (2021b). Biological normativity: a new hope for naturalism? *Medicine, Health Care and Philosophy* 24, 291–301.
- Veit, W. (2021c). The evolution of knowledge during the Cambrian explosion. *Behavioral and Brain Sciences* 44, e47.
- Veit, W. (2021d). Experimental philosophy of medicine and the concepts of health and disease. *Theoretical Medicine and Bioethics*.
- Veit, W. (2021e). Samir Okasha's Philosophy. *Lato Sensu: revue de la Société de philosophie des sciences* 8(3), 1–8.
- Veit, W. (2021f). Scaffolding Natural Selection. *Biological Theory*, 1–18.
- Veit, W. (2022a). Consciousness, complexity, and evolution. *Behavioral and Brain Sciences* 45, e61.
- Veit, W. (2022b). *Health, Agency, and the Evolution of Consciousness*. Ph. D. thesis, The University of Sydney. Manuscript in preparation.
- Veit, W. (2022c). *A Philosophy for the Science of Animal Consciousness*. Book manuscript in preparation.
- Veit, W. (2022d). Revisiting the Intentionality All-Stars. *Review of Analytic Philosophy* 2(1), 1–24.
- Veit, W. (2022e). Towards a Comparative Study of Animal Consciousness. *Preprint*.
- Veit, W. (forthcoming). Review of Peter Godfrey-Smith's *Metazoa: Animal Minds and the Birth of Consciousness*. *Philosophy of Science*.
- Veit, W. and H. Browning (2020a). Perspectival pluralism for animal welfare. *European Journal for Philosophy of Science* 11(1), 1–14.
- Veit, W. and H. Browning (2020b). Two Kinds of Conceptual Engineering. *Preprint*. <http://philsci-archive.pitt.edu/17452/>
- Veit, W. and H. Browning (2021a). Developmental Programming, Evolution, and Animal Welfare: A Case for Evolutionary Veterinary Science. *Journal of Applied Animal Welfare Science*, 1–13.
- Veit, W. and H. Browning (2021b). Extending animal welfare science to include wild animals. *Animal Sentience* 7(20), 1–4.
- Veit, W. and H. Browning (2021c). Phenomenology Applied to Animal Health and Suffering. In S. Ferrarello (Ed.), *Phenomenology of Bioethics: Technoethics and Lived-Experience*, pp. 73–88. Springer.
- Veit, W. and H. Browning (forthcoming a). Life, Mind, Agency: Why Markov Blankets Fail the Test of Evolution. *Behavioral and Brain Sciences*.

- Veit, W. and H. Browning (forthcoming b). Pathological Complexity and the Evolution of Sex Differences. *Behavioral and Brain Sciences*.
- Veit, W. and H. Browning (forthcoming c). The Scaffolded Evolution of Human Communication. *Behavioral and Brain Sciences*.
- Veit, W. and B. Huebner (2020). Drawing the boundaries of animal sentience. *Animal Sentience* 29(13).
- Veit, W. and D. Spurrett (2021). Evolving resolve. *Behavioral and Brain Sciences*, 44, E56.
- Waggoner, B. (2003). The Ediacaran biotas in space and time. *Integrative and Comparative Biology* 43(1), 104–113.