



# Towards a Comparative Study of Animal Consciousness

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## Abstract

In order to develop a true biological science of consciousness, we have to remove humans from the center of reference and develop a bottom-up comparative study of animal minds, as Donald Griffin intended with his call for a “cognitive ethology.” In this article, I make use of the pathological complexity thesis (Veit 2022a, b, c) to show that we can firmly ground a comparative study of animal consciousness by drawing on the resources of state-based behavioral life history theory. By comparing the different life histories of gastropods and arthropods, we will be able to make better sense of the possible origins of consciousness and its function for organisms in their natural environments.

**Keywords** Animal consciousness · Arthropods · Comparative cognition · Evolution of consciousness · Gastropods · Insects · Sentience

*Most of Darwin’s basic ideas about evolution are now generally accepted by scientists, but the notion that there has been evolutionary continuity with respect to conscious experiences is still strongly resisted. Overcoming this resistance may be the final, crowning chapter of the Darwinian revolution.*

Griffin (1998, p. 14)

## Prelude

This article is a philosophical contribution to the science of animal consciousness—a science that the prominent American ethologist and discoverer of bat echolocation Donald Griffin tried to establish in the 1970s when he called for a “cognitive ethology,” but which only truly began to take shape as a genuine interdisciplinary field a decade after his death with the “Cambridge Declaration on Consciousness” in 2012 and the formation of the first interdisciplinary journal of nonhuman consciousness in 2015, aptly titled

“Animal Sentience”<sup>1</sup> (Browning and Birch 2022; Browning and Veit 2022). As per the epigraph featured above, this article will try to help the realization of Griffin’s vision of the “final, crowning chapter of the Darwinian revolution” by helping this burgeoning field to cast off the chains of a pre-Darwinian view of the mind in both philosophy and science and begin a transition towards a true Darwinian science of consciousness in which its evolutionary origin, function, and phylogenetic diversity are moved from the field’s periphery to its very center.

In order to develop a true biological science of consciousness, we must attend to the (cognitive) ethologist’s demand to address the *functionalist question* of what consciousness in all of its diversity and gradations does for healthy agents in the pursuit of their life history strategies. Accordingly, an evolutionary approach to consciousness has two objectives: (1) to demonstrate the possibility of a comparative bottom-up approach that addresses the problem of consciousness in terms of the evolutionary origins of a

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<sup>1</sup> See Veit and Harnad (2020) and Veit and Rowan (2020) for interviews with its editors.

new life history strategy that made consciousness worth having, and (2) to articulate a thesis and beginnings of a theory of the place of consciousness as a complex evolved phenomenon in nature. The thesis that I have developed for such an evolutionary approach to consciousness is what I have dubbed “the pathological complexity thesis” (Veit 2022a, b, c). It can be succinctly summarized as follows:

**The Pathological Complexity Thesis:**

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

Pathological complexity can simply be understood as the computational complexity of the economic trade-off problem between competing actions faced by all organisms as they deal with challenges and opportunities throughout their life cycle in order to maximize their fitness. This ecological notion of biological complexity is inherently evaluative and will vary according to the different life histories of different animals, dynamically emerging from the interaction of organism and its environment (see also Veit and Browning 2022).

To provide a one-paragraph summary of the pathological complexity thesis: my framework is intended as a rejection of the false dilemma between the two dominant traditions in philosophy of mind and the science of *human* consciousness, between strongly externalist representationalist theories of consciousness that overemphasize sensory experience and strongly internalist ones that overemphasize self-awareness as the models for all of experience. Instead, I aimed to develop an alternative model of consciousness based on a model of *evaluative experience*, which can be described as an inherently “interactionist” or perhaps better a “dynamic” dimension of consciousness.

In both my dissertation (Veit 2022c) and a compendium article to this article (Veit 2022a) I have offered a defense of why the Cambrian explosion led to the dawn of a new sentient life history strategy. This new mode of being led to individuals capable of feeling positive and negative experience (hedonic valence)—a capacity evolved for efficient action selection that quickly became more representational due to increases in discriminatory capacities, thus ultimately giving rise to sensory experience and “points of view” as evolutionary transformations of more basic *Benthamite creatures* only capable of evaluative experience.<sup>2</sup>

While the original sentient beings plausibly had simple hedonic evaluations (whether positive or negative) of their current situation that compelled them towards particular actions, this capacity would have transformed “quickly” over the next millions of years. Evaluations of particular

states would come to be associated with their own phenomenological character to enable the comparative evaluation of tradeoffs and associative learning. If this account for the core and origins of consciousness is on the right track, we will be able to make predictions about the phenomenological complexity of other animals through an analysis of the pathological complexity (or life history complexity) of their species-specific lives, thus enabling us to develop a comparative bottom-up study of consciousness just as Donald Griffin intended with his call for a cognitive ethology.

The goal of this article will be to put the pathological complexity thesis to the test, both as a framework for a bottom-up comparative study of animal consciousness, and as a hypothesis about the core and origins of consciousness being found in hedonic valence. I will do so by responding to a suggestion by Godfrey-Smith (2020a, b) that there could be a phylogenetic split between the extant conscious animals, with some animals having evaluative experience while lacking the sensory experience and vice versa. Could there be a dissociation between these dimensions such that some animals only have sensory experience?

If we find animals for which this is the case, that would at least raise an interesting challenge to the pathological complexity thesis, since my theory locates minimal consciousness in evaluation and treats sensory experience as an evolutionary “add-on,” once the basic evaluative capacities gain discriminatory and representational richness (Veit 2022 c). Sensory experience is simply an outcome of an increase in evaluative complexity that allows for more stimuli to be distinguished, assigned value, and compared to enable efficient action selection. This account provides us with an explanation for why some sensory states have a subjective “feel” to them, making hedonic evaluation a prerequisite for sensory experience. Information-processing complexity in the sensory processes of an organism alone is not sufficient to give rise to minimal consciousness in the sense of qualitative experience, which is why Godfrey-Smith’s arguments for a phylogenetic split constitute an interesting challenge.

To investigate this potential counter to the pathological complexity thesis, we will firstly look at the gastropods (snails and slugs) and secondly the arthropods (in particular crustaceans and insects) that are used in Godfrey-Smith’s case for a phylogenetic split. Admittedly, only insects constitute a real counterexample because Godfrey-Smith (2020b) uses gastropods as a potential case where the sensory side appears to be very simple but “may have relevant evaluative complexity” (p. 1153). Indeed, my discussion of gastropods will primarily serve as evidence *for* the pathological complexity thesis: the possibility of minimal consciousness in the sense of hedonic valence, without other dimensions of consciousness being present. This is entirely

<sup>2</sup> I call these Benthamite after the father of utilitarianism Jeremy Bentham, who argued that animals and humans act to maximize their hedonic wellbeing. The evolution of these creatures will also be the subject of a future book on animal consciousness (Veit 2022d).

compatible with the pathological complexity thesis, and in fact lends support to it, since it would increase our credence for thinking that evaluative experience could exist without the sensory side of things. In insects, however, Godfrey-Smith maintains that they only have simple evaluative capacities, whereas their sensory capacities are sufficiently rich to make it at least plausible that they could have sensory experience without the evaluative side. Reviewing the evidence of the literature for this view, I will ultimately reject it, arguing that insects have sufficient evaluative complexity to undermine the view that they could have consciousness without the capacity to have positive or negative feelings. Admittedly, little attention has so far been given to the gastropods and arthropods in discussions of animal consciousness, but we can use the pathological complexity framework alongside recent evidence to move us further towards understanding what it is like to be *them*.

## Article Outline

This article is structured as follows. In the second section, “Gastropods: A Sluggish Way of Life,” I use the case of gastropods to support the motivation of the pathological complexity thesis in seeking the origins of consciousness in evaluation. Indeed, they serve as plausible model organisms to study the origins of sentience, with the other dimensions idealized away by nature itself. In the third section, “Arthropods: A Robotic Way of Life,” I respond to the challenge that insects might have sensory experience without evaluative experience and argue that even land insects share many similarities with the life histories of crustaceans, which should provide evidence against the idea that insects do not have evaluative experience, even if they do not feel pain. Pain may be the human paradigm for hedonic valence, but thirst, hunger, and other evaluative processes such as learning, alongside other long-term states, may be present even in its absence. Finally, the fourth section, “Conclusion and Further Directions,” will summarize the arguments of this article, offer some responses to potential objections, and explore potential directions for the further development of the pathological complexity framework for a comparative study of animal consciousness.

## Gastropods: A Sluggish Way of Life

The first class of animals we shall discuss are gastropods (i.e., snails and slugs) which, like cephalopods, are molluscs, though they generally differ in nervous system complexity. Unlike cephalopods, and in particular octopuses (Mather 2008; Browning 2019a; Jacquet et al. 2020; Schnell et al. 2022), gastropods have received little attention in debates

on animal consciousness. Their lives appear too slow, too uninteresting, compared to the extreme behavioral flexibility, tempo, and intelligence of their octopus relatives. One might thus be tempted to categorize their pathological complexity as nonsignificant, but that would be a mistake. As Dennett (2019) once warned, our imagination is in many ways shaped by what Wittgenstein dubbed *Lebensform* (form of life), that is, “our linguistic communities, the commonalities that are apt to confound our thinking with parochiality” (p. 2). If we observe animals only distantly related to us and with very different ways of life, we will be influenced by what Dennett nicely expressed as their *behavioral rhythm and speed*:

[I]f cephalopods moved in the clunky way of most existing robots, then in spite of the manifest purposiveness of their motions, it would be quite comfortable to suppose that they were some kind of zombies, marine robots with eight or ten appendages. (Dennett 2019, p. 2)

Gastropods, of course, appear even slower than many sophisticated robots. Care must be taken not to deny them consciousness simply because they are different. Prominently, Feinberg and Mallatt (2016) argue that evidence for consciousness in gastropods is lacking, but they also admit that there is some evidence pointing towards the affective side. However, they end up denying consciousness to gastropods since they are said to “lack the brain complexity one would expect for consciousness” (2016, p. 192). This, of course, raises the question of whether we already know what brain complexity would be necessary. Godfrey-Smith (2020b) evaluates the evidence in a different way by emphasizing that gastropods may be a case with sufficient richness in evaluative capacities to have evaluative consciousness while lacking the other dimensions. If so, this would provide strong support for the pathological complexity thesis: we could have animals around us in the here and now, rather than just at the origin of consciousness in the Cambrian, with a minimal sense of hedonic evaluation without the other dimensions. A theory of consciousness based on the human case is undoubtedly prone to fail in its recognition of such “marginal” cases, so it is useful to examine their life histories from their own point of view by using the pathological complexity framework.

## Evaluative Experience

In his emphasis on the evaluative capacities of gastropods, Godfrey-Smith draws especially on the work of Terry Walters, who has been one of the frontrunners in advancing our

understanding of gastropod *skills*.<sup>3</sup> Notably, we should not simplify this dimension to only pleasure and pain. These are often used in a very deflationary sense for any sort of subjective experience that has a positive or negative valence (see also Browning 2020). For obvious reasons this can mislead others to needlessly restrict this dimension, missing out on medium-term and long-term states such as emotions of anger or fear. As we will also see in the following discussions of insects, we should be open to the existence of all kinds of negatively valenced states, and not limit them to human-like cases of pain involving rich sensory representation.

Crook and Walters (2011), for instance, argue that gastropods show *nociceptive sensitization*, which Godfrey-Smith (2020b) describes as “a heightened sensitivity after damage” (p. 1155) and sees as compelling evidence for perhaps a minimal sense of evaluative experience. What this work has shown is that when gastropods are exposed to aversive stimuli such as electric shocks, they not only react with an immediate behavioral response, but there also appears to be a long-term change in behavioral “character.” Crook and Walters (2011) argue that *Aplysia* show a conditioned fear-like motivational state when exposed to neutral chemosensory stimuli such as a touch when it has in the past been associated with an electric shock (p. 189). Indeed, already in 1981 Walters had shown that gastropods have the capacity for associative learning (see Carew et al. 1981; Walters et al. 1981; Colwill et al. 1988), thus suggesting an underappreciated level of evaluative richness that may be indicative of sentience.

When the smell of a shrimp was paired with an electric shock, *Aplysia* showed surprising results in response to these stimuli in the future, such as (1) freezing in response to the smell even in the absence of electric shocks, (2) halting of feeding when exposed to the smell, and (3) withdrawal, escape, and defense responses when the smell was paired with light touch (Crook and Walters 2011, p. 189).

From exchanges with Walters, Godfrey-Smith reports that Walters is more cautious about attributing sentience to *Aplysia*, but that he also acknowledges the striking functionalist rationale of an “ability to maintain functional ‘awareness’ of injury-induced vulnerability until the vulnerability subsides (perhaps until adequate repair of damaged body parts has been achieved)” (Walters 2018, p. 13; cited in Godfrey-Smith 2020b, p. 1155). So, it is hardly surprising that Godfrey-Smith (2020b) rightfully characterizes this surprising range of evaluative responses as compelling evidence for a “pervasive state of negative readiness” linked to the feelings side of subjective experience (p. 1155).

If the pathological complexity thesis is right, then this is exactly how the vulnerability of complex multicellular

organisms gives rise to hedonic experience. One may even see these negative mood states as involving a minimal sense of self and a sense of time. But these features need not be part and parcel of the subjective experience of an animal in order to make particular stimuli associated with a negative valence. After all, even humans can have a negative emotional reaction to an event or food item without the ability to consciously draw the connection to a negative encounter in the past. Nevertheless, it is tempting to think that episodic memory can be readily explained as something built on these capacities once they are in place and we should resist the thought that current boundary cases for the attribution of sentience must be anything like the animals in the early evolution of subjective experience. It is not at all implausible to think that the presence of a hedonic evaluation system quickly gives rise to further increases in phenomenological complexity.

Furthermore, Godfrey-Smith (2020b) praises Walters for highlighting the distinctive life histories of *Aplysia* which often involve longer life cycles, of one to two years more than is common in many insects. If we try to explicate the pathological complexity of gastropods one will quickly find an additional rationale for these long-term mood states. Because their behavior is relatively limited in comparison to many other animals that are discussed as potential bearers of sentience, wound tending does not appear to be within their option space. Yet that doesn’t mean that gastropods aren’t vulnerable. Unlike insects whose bodies are hard, many slugs and snails lack even shells to protect themselves. But whereas insect bodies can often not be “repaired,” hence making protection superfluous, gastropods almost constitute a polar opposite case, with excellent if not extreme abilities to heal. As long as wounds are not mortal, they will quickly restore their bodies to a healthy state of normalcy again.<sup>4</sup> An extraordinary case in the genus *Elysia* cf. *marginata* reported by Mitoh and Yusa (2021) has recently gained a lot of attention, since these slugs have been shown to be able to decapitate their own heads from their body, which includes shedding the entire heart, in order to rid themselves of a potentially parasite-infested body. This is an extreme case of *autotomy* (i.e., the not-uncommon behavioral strategy of deliberately shedding body parts or self-amputation), enabled by the special regenerative modes of being of gastropods. This is one way of responding to the pathological complexity of the gastropod life cycle. But it is also precisely in this context in which behavior is limited, and bodies are vulnerable yet allow for healing, that it makes sense to invest both in short-term states of pain and in longer-term mood states such as fear or pessimism. Note that I am here not arguing for the thesis that they must be conscious, only

<sup>3</sup> See Walters (2018) for a recent review.

<sup>4</sup> I am here employing a naturalistic sense of health (see Veit 2021).

that we have to think about their life histories to even begin to think about what kinds of subjective experience it would be worth having. Not too much should be made here out of the associations with certain rich human emotions and mood states. What we are interested in are these states as natural phenomena, which makes the human case a special case.

Due to the small nervous system that has made *Aplysia* a model organism to begin with, these results provide compelling functional evidence that a minimal degree of sentience may be present in these slow and vulnerable creatures. This view isn't anti-neural as much as it is gradualist. Because the genus *Aplysia* includes the largest sea slugs, especially sea hares (*Anaspidea*) among which the California sea hare (*Aplysia californica*) stands out in particular, for these comparatively much more active and mobile agents—their movement resembling a “gallop rather than a slow crawl,” as Godfrey-Smith notes—it can be hard not to grant them experience (2020a, p. 216). But despite their behavioral difference from smaller sea slugs that have very similar nervous systems yet lack this intuitive compellingness to be attributed sentience, this may have merely been one of perspective, with Godfrey-Smith arguing that once they are scaled up to the largest among the *Aplysia*, it becomes hard to draw a hard boundary of experience; doubly so if their movement is sped up. A gradualist picture is tempting here, and fits better with the actual data than the demand for a hard line (Veit and Huebner 2020). Even tiny slugs and their ancestors may possess a basic capacity for evaluative experience, despite a lack of capacities on the other dimensions. But let us examine the sensory side of experience as well, in order to make sure that they do only have evaluative experiences.

### Sensory Experience

In the previous section I mentioned that gastropods seem to have fewer degrees of freedom in their behavioral repertoires compared to insects. Furthermore, they have much simpler sensory capacities, though there are some exceptions. Godfrey-Smith (2020b), for instance, notes that sea elephants or heteropods (*Pterotracheoidea*) have something of a borderline case of class IV eyes, i.e., high-resolution vision, which might provide compelling evidence for sensory experience on the visual side. What also distinguishes the lifestyles of these species is that they are much more mobile; they have fins for free swimming and engage in predation, in contrast to most gastropods that live on the ground. The pathological complexity they are faced with is quite different from the usual sluggish gastropod way of life. For these swimming gastropods, with lifestyles more closely resembling the pathological complexity of fish and

cuttlefish, we can make predictions regarding the likely richness in their sensory experience. If sensory information processing (whether conscious or nonconscious) is found in various degrees of complexity within a branch of life that is already a likely contender for minimal sentience due to their rich evaluative capacities, the pathological complexity thesis appears to gain striking support for the close relationship between complex life histories and evaluative experience. Sensory experience may be important for many evaluative capacities of consciousness, but it does not appear to be necessary and should be seen as an enrichment that pays off with higher degrees of pathological complexity that make sensory experience *worth having*.

After all, as life histories become more complex, and thus involve greater pathological complexity, the evaluative experience of organisms is bound to benefit from greater discriminatory capacities to allow for the distinguishing of different stimuli, their evaluation, and ultimately their comparison in order to optimize action selection. Most gastropods, however, appear to only have a “sliver of the features that make for experience in us” (Godfrey-Smith 2020a, p. 262), and this sliver appears to be mostly on the evaluative side, thus providing compelling evidence for the independent existence of evaluative experience without strongly representationalist sensory capacities. Let us now turn to the case of insects which, if Godfrey-Smith is right, may undermine the pathological complexity thesis due to their possession of sensory without evaluative consciousness.

### Arthropods: A Robotic Way of Life

Whereas Godfrey-Smith's (2020b) arguments for the presence of evaluative experience in gastropods without the sensory side provides strong support for the pathological complexity thesis, his arguments for the existence of sensory experience without the evaluative side in insects provides an interesting challenge to the idea that the core of consciousness is to be found in evaluation, which we will ultimately have to overcome. Godfrey-Smith (2020b) suggests that complexity in sensory “capacities might be understood as involving complexity in discrimination or in downstream processing” (p. 1153), but emphasizes the latter as being more important for considerations of subjective experience. That is certainly reasonable due to a recognition of how many discrimination activities are going on without subjective experience even in humans, but Birch et al.'s (2020) dimensions of animal consciousness characterize evaluative richness as complexity in discrimination. For the purposes of the discussion here, I agree with Godfrey-Smith's emphasis on downstream processing, since the pathological complexity thesis sees sensory experience as



something operating within an evaluative sphere. It is only in this hedonic context that these sensory processes are *felt*, rather than any and all cognitive processes involving discrimination.<sup>5</sup> Let us therefore now closely examine the challenge that sensory experience could exist without such an evaluative space in which different sensory stimuli are being evaluated against each other.

Insects are part of the arthropod branch of life and constitute the great majority of arthropod species (in addition to all animals!), but are estimated to have originated only roughly 479 million years ago during the early Ordovician. This, as Misof et al. (2014) point out in a landmark study in *Science*, suggests that they have evolved in response to the plants that started to colonize the planet around the same time (see also Labandeira 2006). However, the arthropod group, which also includes crustaceans (e.g., crabs, lobsters, and krill), arachnids (e.g., spiders and ticks), and myriapods (e.g., centipedes), are a much earlier Cambrian invention; indeed they constitute the paradigm phylum of the Cambrian explosion, leading the way for a special animal way of life. Their name, a conjunction of the Ancient Greek words for “joint” and “foot,” is a fitting description for a mobile mode of being consisting of hard shells, multiple segments, and typically many appendages (Budd and Telford 2009), that nevertheless shares a common active lifestyle with the “soft” and “sluggish” gastropods. But despite sharing a high degree of pathological complexity, it plays out differently in both groups, and this might make it tempting to think that arthropods could evolve sensory consciousness without the presence of evaluation. To examine this further, we will this time begin with the sensory side of consciousness.

## Sensory Experience

Unlike the soft-bodied gastropods, arthropods seemingly overflowed in the Cambrian, with trilobites making up much of the fossil record. Partially this is due to their possession of an exoskeleton, which simply fossilizes better, but their presence emphasizes much of the change that took place during the Cambrian. An exoskeleton makes *sense* as a protective shell against others, with appendages such as feelers and claws clearly existing in response to other subjects, whether prey, partner, or predator. Godfrey-Smith (2020a) describes arthropods as having “invented a new way of being an animal, with a skeleton that scaffolds and organizes complex actions. They also invented claws, and to go with them, image-forming eyes” (p. 80). All this appears much richer than the sensory capacities and behavioral repertoire of gastropods and it is not surprising that Feinberg and Mallatt (2016) in their evolutionary overview also

emphasize this richness. These facts may actually make it surprising that few have granted them a minimal sense of subjective experience despite the vision-centric model of consciousness that is prevalent, since many insects have been shown to have sophisticated sensory capacities and especially high-resolution vision. Again, I want to note that I am here not arguing for the thesis that arthropods necessarily have consciousness, only that *if they do* they are likely to have sensory as well as evaluative experience, rather than just the sensory side.<sup>6</sup>

Godfrey-Smith (2020b) focuses especially on the much-studied bees and fruit flies (*Drosophila*), since it is here that we can examine flight as a complex behavior that “involves dealing with complex spatial layouts and making self/other distinctions with respect to the causes of sensory events” (p. 1153). Indeed, in the ecological framework for the comparative study of consciousness that I try to build, flight constitutes the paradigm case for an explosion in pathological complexity. Godfrey-Smith doesn’t commit himself here but sees the sensory processing of flying insects as a plausible candidate for subjective experience. That flying creates a new challenge of complexity is not a new idea.

In his very first publication, the British evolutionary biologist and former aeronautical engineer Smith (1952) already emphasized the importance of a sophisticated nervous system in the evolution of flight, for both birds and insects. He argued that the evolutionary origins of flight must have required flight stability via a long tail, since they lacked the sensory richness and nervous system complexity to control such a flying body, similar to how pilots require a stable plane in order to be able to fly it. While such a tail lowers maneuverability, it greatly increases flight stability. Yet Maynard-Smith argued that “in the birds and at least some insects, and probably in the later pterosaurs, the evolution of the sensory and nervous systems rendered the stability found in earlier forms no longer necessary” (1952, p. 129). The evolutionary advantages of unstable flight, he argued, would be the ability to turn more rapidly in the air and to be able to fly at slower speeds without falling (1952, p. 128). Taking a design stance toward the problem of flight makes it obvious how rich the complexity of this problem really is. Free fall can mean death. But Maynard Smith made these comments in relation to birds. Because insects are so small, air resistance will stop them from gaining enough fall speed to cause serious injury. Nevertheless, it is precisely because of their size that it is more important to focus on the

<sup>5</sup> A related problem is the misidentification with cognitive complexity, or “intelligence” with sentience (Browning 2019b).

<sup>6</sup> While the pathological complexity thesis certainly increases the credence for the presence of sentience in insects, their very small nervous systems may provide a compelling reason to think that at least some branches of insect life might have lost consciousness. The minimal nervous system requirements for sentience will be a matter for another paper.

organization of the insect nervous system, rather than the mere number of neurons. Regardless of the possible challenges that can be raised to the presence of sensory consciousness in arthropods and/or flying insects, however, it (1) makes sense within the pathological complexity framework and (2) will be accepted in order to tackle Godfrey-Smith's challenge that the sensory side could exist without the evaluative side.

## Evaluative Experience

In order to make his case for a potential separation of the evaluative and sensory sides of experience in insects, Godfrey-Smith draws on an old but influential mini-review by Eisemann et al. (1984) in order to establish that “all known insects appear completely unconcerned about even severe body damage. Wound-tending has never been seen in an insect, and after injury these animals just continue, as best they can, with the behavior appropriate to the circumstances” (Godfrey-Smith 2020b, pp. 1153–1154). But this is partially a misrepresentation of even this early work on the possibility of insect pain. Indeed, Eisemann et al. (1984) cite early experimental work by the German zoologist Erwin Hentschel (known in Germany as the “bee professor”<sup>7</sup>) that showed grooming activity in response to damage (Hentschel et al. 1982) as something to be *explained*. They explicitly recognize an “increase in both general grooming activity and specific grooming of a wound site observed after experimental puncturing of the abdominal wall of the cockroach *Periplaneta americana* (L.)” (1982, p. 166).

While it is true that Eisemann et al. (1984) argue that insects do not feel pain, they do so in a very measured way, only stating that “the evidence from consideration of the adaptive role of pain, the neural organisation of insects and observations of their behavior does not appear to support the occurrence in insects of a pain state, such as occurs in humans” (p. 167). That they see the evidence as far from conclusive is also emphasized by their call to endorse Wigglesworth's earlier

recommendation that insects have their nervous systems inactivated prior to traumatizing manipulation. This procedure not only facilitates handling, but also guards against the remaining possibility of pain infliction and, equally important, helps to preserve in the experimenter an appropriately respectful attitude towards living organisms whose physiology, though different, and perhaps simpler than our own, is as

yet far from completely understood. (Eisemann et al. 1984, p. 167)<sup>8</sup>

This makes it somewhat puzzling as to why Godfrey-Smith (2020a) similarly repeats his assertion in *Metazoa* that “insects have still never been observed tending and grooming injuries; that claim from the old no-pain paper still holds up” (pp. 211–212).<sup>9</sup> Just because insects have not been shown to engage in sophisticated “protective behavior towards injured body parts, such as by limping after leg injury or declining to feed or mate because of general abdominal injuries” (Eisemann et al. 1984, p. 166) does not mean that no grooming-like behavior has been observed—even if it could be explained in a way unrelated to pain. The way Eisemann et al. (1984) deal with Hentschel's observations is to point out the “contra-adaptiveness of this response in relation to wound healing” (p. 166). But we have to distinguish the adaptive value of such behavior from its support for the presence of subjective experience. It may very well be the case that not all grooming behavior is adaptive, no less so than itching or scratching of human wounds is. Pain could be invoked as a cause as long as a general negative valence exists regarding damage or potential damage. Indeed, this might even be seen as supporting the presence of negative valence as opposed to a mere “mechanical” response.

My argument here, however, should not be read as me endorsing the presence of pain in insects. I only argue that the case is not as straightforward in insects as Godfrey-Smith makes it seem. Nevertheless, it is certainly true that insects—more so than perhaps any other complex agent-like animal group—have been observed to be apparently oblivious to all kinds of damages and injuries and such findings as well as anecdotes certainly constitute important evidence (Browning 2017). They engage in sex and eating while being devoured, soldier on despite damages, and even eat their own insides when they are leaving behind their body due to damage (Eisemann et al. 1984; Adamo 2016; Walters 2018). There appears to be a striking failure to recognize biological normativity in insect life. In order to understand whether such behavior is functional or not, we will have to understand the pathological complexity faced by insects. Godfrey-Smith (2020b) notes the “ecology of insects is also relevant” (p. 1154), but for a true cognitive ethology it should be our primary source of information. Godfrey-Smith's (2020b) references to the life history of

<sup>7</sup> <https://idw-online.de/de/news15923>.

<sup>8</sup> See also Wigglesworth (1980).

<sup>9</sup> In personal communication (14 Aug 2021) Godfrey-Smith admitted that he should not have used the term “grooming” in his list and aims to have it removed in a second edition of his 2020b book *Metazoa* (see also Veit 2022e for a review of his book).

insects versus crustaceans is particularly interesting here in the context of the pathological complexity thesis.

Whereas most crustaceans live in the water, having similar life history strategies to their Cambrian ancestors, the insects have predominantly branched towards a life on land.<sup>10</sup> Yet whereas Godfrey-Smith wants to deny evaluative experience in insects, he grants it to crustaceans, where wounding has been firmly established. The work of Elwood and his collaborators (Appel and Elwood 2009; Elwood et al. 2012) has studied the evaluative trade-offs crustaceans are engaged in, particularly decapod crustaceans (shrimps, crabs, and the like). Hermit crabs have shown, for instance, that they are making state-based decisions on whether or not to leave their shell when receiving electric shocks, dependent upon both the predicted presence of predators and the shell value. Furthermore, in a recent extensive review that has led to decapod crustaceans being included in the animal sentience legislation in the UK, a wealth of data has been presented to support sentience in these creatures (Birch et al. 2021; see also Crump et al. 2022).

But this admittedly transforms the challenge to the pathological complexity thesis. Instead of sensory experience arising independently in its own right, the challenge now appears to be explaining a loss of the evaluative side once the sensory side has come to play a more important role. After all, these results have motivated Tye (2016) to call his book *Tense Bees and Shell-Shocked Crabs: Are Animals Conscious?* to begin with. But Tye has of course neglected the importance of the underlying state-based behavioral and life history theory in favor of his much more simplistic epistemological “defeater” approach. Allen and Bekoff (1997, p. 153) criticized as anti-neural Griffin’s suggestion that bees might have more of a use for subjective experience *because* their nervous systems are so small, but it is based on the important insights of Lorenz and Tinbergen for putting a firm understanding of the animal’s life history prior to laboratory experiments.

Within the peculiar pressures of life on land, most insects have evolved short and routinized lives that differ from the comparatively longer and “less regimented lives of their marine relatives studied by Elwood” (Godfrey-Smith 2020b, p. 1154). While there are exceptions to this rule (Maruzzo and Bortolin 2013; Suzuki et al. 2019), insect limbs generally do not regrow and there is little evidence that there is adaptive value for them in protecting injuries. Godfrey-Smith (2020b) describes this lifestyle as being about *soldiering on* even in the face of pathologies (p. 1154). Now, this makes sense in a semelparous life and especially so in eusocial insects where individuals can be replaced. One might expect bees or ants to have sophisticated sensory

capacities for finding food sources but being less rich on the sensory side *in order to* focus on their task. But does this really show that the evaluative side has been lost?

Godfrey-Smith (2020b) admits that bees have been shown to avoid noxious stimuli such as heat, but notes that this could be a mere reflex, not necessarily involving subjective experience. A compelling line of evidence in this context is various kinds of learning, since they are commonly taken to increase our confidence in attributing evaluative experience. Also highlighted by Godfrey-Smith is reinforcement learning which has been shown in various insects (see Allen et al. 2005; Elwood et al. 2012) and is often drawn on in discussions of consciousness. Which forms of learning constitute the best kinds of evidence is, however, contested.<sup>11</sup> But as with gastropods, we should also highlight evidence for nociceptive sensitization as indicative of evaluative richness in insects, which is also noted by Tye (2016). One peculiar result that Godfrey-Smith (2020b) highlights is the presence of sensitization in *Drosophila* larvae, as opposed to its later life stages (p. 1156). Too much focus, he notes, might have been given by Eisemann et al. (1984) and Groening et al. (2017) to the absence of pain in adults:

Another factor in insects not highlighted so far, one related to life on land, is the differences between larval and adult states. Many insects lead two lives, in effect, one on each side of a metamorphic divide, with extensive breakdown and reconstruction at that stage. In the kinds of insects considered here, it is the adult who has acute sensing that controls complex motion; the larva does not. (Godfrey-Smith 2020b, p. 1156)

Drawing on Sprecher et al. (2011), Godfrey-Smith emphasizes that larvae have very simple eyes—in *Drosophila* only the small number of 12 photoreceptor neurons dedicated for vision, much simpler than the adult stages. Yet, in contrast to the apparent obliviousness to damage in adult insects, Godfrey-Smith (2020b) also highlights work by Walters (2018) that showed larval stages of *Manduca* and *Drosophila* to have nociceptors and nociceptive sensitization. What we find in insects is a striking disconnect between the pathological complexity faced by the larval and the adult stages.

<sup>10</sup> Crustaceans are likely a paraphyletic group (Blackstone 2001).

<sup>11</sup> Ginsburg and Jablonka (2019) provide a good overview of this debate and argue that there is a form of learning that they dub “unlimited associative learning” (UAL) that provides something like a proof that animals are conscious, though they do not mean to say that the absence of UAL shows that consciousness isn’t present. I am very skeptical that we can actually find anything like a definite marker, since consciousness can come in a diversity of forms, but that is not an objection to the idea that sophisticated associative learning would constitute a good indicator for a certain richness or even transition of consciousness, as opposed to its presence (see Browning and Veit 2021 for a review of their work).



As Walters (2018) observes: “Trade-offs between survival and reproductive success are found in all animal groups but seem especially striking in insects” (p. 12).

In part, such observations are due to the extreme diversity of insect life, which explains the presence of a huge variety of alternative behavioral life history strategies; including such odd examples as male mantids engaging in sex with females despite being eaten afterwards. While this behavior may well be adaptive (Schwartz et al. 2016; Zuk 2016), it is hard to think about such extreme behaviors involving pain. And yet, larvae—despite their nervous system simplicity—often appear to have richer evaluative capacities than adults, indicative of the different emphasis of survival during this stage, as opposed to reproduction in the adult one. The adult insect body is described by Godfrey-Smith (2020b) as a mere tool for this end. So, it would make sense to have life-stage-dependent varieties of experience. This is something that can straightforwardly be captured within the pathological complexity framework, providing us with a measure for the different stages of a life history (though I will not go into the mathematics here). Indeed, we can use this framework to integrate work on the mechanism, development, function, and evolutionary history of consciousness.

A recent compelling case for insect consciousness has been made by Barron and Klein (2016), yet they largely emphasize the sensory side of things. Findings of the evaluative side are more compelling than they are typically given credit for. Godfrey-Smith (2020b) points to self-administration of analgesics which has been used as compelling evidence of pain in birds and fish, yet has not been found in bees (Groening et al. 2017), but that is not the only source of evidence we can look for. Bateson et al. (2011) show convincingly that bumblebees, if they have been shaken, can have negative long-term mood states called pessimistic bias. Similarly, Godfrey-Smith (2020b) admits that bees and other insects show aversive responses to heat, which may be better stimuli to look for the presence of subjective experience.

As I have argued elsewhere, even if insects do not experience human-like pain towards mechanical injuries, they may very well experience other aversive experiences such as hunger or thirst (Browning and Veit 2020a). The absence of pain is too often confused with the absence of evaluation. But the lifestyles of insects simply don't make it necessary to put much of a value on protecting one's bodily shell from mechanical damage. What is important is to complete one's life history strategy: i.e., to reproduce. If wounding doesn't aid that, there is little sense in putting much valence on it. Instead of focusing on pain-like behavior as an admittedly tempting but flawed paradigm case of evaluative experience, we should look at evidence for a valence system more generally that evaluates trade-offs between

conflicting stimuli in a flexible manner. Evidence that is very compelling here, and highlighted by Godfrey-Smith (2020b), is a follow-up study to Bateson et al. (2011), which focused on positive mood states in the form of optimism bias in response to unexpected rewards in bees (see Perry et al. 2016). The idea of pleasure as a common currency for affective decision-making is sometimes criticized as failing to account for the different neural mechanisms of negative and positive evaluation, but such common functional roles of evaluation suggest that they are deeply evolutionarily intertwined. Indeed, they must largely operate in tandem to allow for efficient decision-making and learning in the face of novel and ambiguous stimuli.<sup>12</sup>

Given how much we know about sensory processing taking place unconsciously in human brains, it appears plausible to think that it is only those sensory inputs that enter the affect system of the brain that are consciously experienced (see also Ginsburg and Jablonka 2019). It provides us with an answer to those who insist that functionalist accounts of consciousness cannot explain the “feel” of experience, since it is precisely this subjective experiencing that does the functional work. It enables organisms to efficiently deal with their species-specific pathological complexity. So while we can readily admit that insects do not feel pain due to their “robotic” way of life, their complex behaviors and learning abilities are highly suggestive of something like a common currency of valence for efficient action selection, even if their evaluative capacities on this side of things may have become poorer compared to their sea-living ancestors. Insects, after all, are in many ways the scaled down versions of their Cambrian ancestors, with a constant pressure for nervous system simplicity, especially in those insects that can fly. It is because of this that they might provide us with an insight into the minimal nervous system requirements for sentience. Lack of evidence should here not be confused with evidence of absence precisely because dedicated research on their evaluative capacities (as opposed to their sensory capacities) has been rare. But this is now beginning to change.

Indeed, on February 8 this year, a particularly compelling preprint on motivational trade-offs in bumblebees was uploaded by Lars Chittka's bee lab (see Gibbons et al. 2022). In it, the authors showed that bees when faced with noxiously heated feeders and different sugar concentrations could trade off “competing conditioned motivational stimuli to modulate nocifensive behaviour” which they argued would suggest “a form of pain perception” (Gibbons et al. 2022, p. 1). This suggests that even the presently best case for the independent existence of sensory experience without

<sup>12</sup> While metaphors can sometimes impede scientific progress (Veit and Ney 2021), the metaphor of a common currency is highly useful to think about the evolution of sentience.

evaluative experience turns out to have rich evaluative capacities after all, supporting the motivation of the pathological complexity thesis to seek the origins and core of subjective experience in hedonic valence without the need for other dimensions of consciousness to necessarily be present (see also Veit 2022 f). Arthropods may have a robot way of life, but that doesn't mean that they do not engage in complex evaluations.

## Conclusion and Further Directions

In this article, I have discussed numerous animals such as snails, slugs, fruit flies, crabs, and bees, that many if not most will suspect not to have sufficient nervous system complexity to warrant an attribution of consciousness. While the scientific assessment of consciousness in nonhuman animals has methodological roadblocks (Browning and Veit 2020b), I hope to have made clear in this article that it is precisely in such comparatively "simple" animals that we have to begin an evolutionary investigation of consciousness. They are the best cues to what the gradual evolution of subjective experience may have been like, providing us with a rich diversity of alternative life history strategies. If these animals are conscious, their consciousness profiles would appear to be restricted to the dimensions of evaluative experience and sensory experience, with perhaps some sophistication on the selfhood side with an implicit distinction between exteroception and interoception (though this could also be seen as richness of the sensory side of things). My discussion here was framed against recent work by Godfrey-Smith (2020a, b) who emphasized the possibility of a disassociation between the sensory and evaluative side in gastropods and insects, which may yield us a two-by-two table representing capacities across each dimension.

Since the pathological complexity thesis seeks to locate the origins of consciousness in evaluation, Godfrey-Smith's analysis of gastropods provides excellent support for the idea that there have been organisms at the beginning of the Cambrian with evaluative capacities sufficient for sentience, but lacking sensory experience. Indeed, such organisms could be around even now, undermining the common idea that consciousness must necessarily involve a great cluster of capacities related to consciousness in humans. Godfrey-Smith's case for the independent existence for sensory experience, however, has constituted an interesting challenge to the pathological complexity thesis, since my framework explained the phenomenal feel of sensory experience as a discriminatory capacity of a more basic evaluative capacity for experience.

As I hope to have shown in this article, however, this second conceivable separation must not constitute a real

separation in nature. Even insects with their apparent disregard for their own bodies seem to have rich evaluative capacities, making the attribution of exclusive sensory experience without evaluation a less promising contender. Whereas most discussions of consciousness focus on animals that plausibly have together at least a minimal sense of both sensory and evaluative experience, such as most vertebrates and octopuses, a comparative bottom-up approach allows us to reverse engineer the origins of consciousness by emphasizing the animals in which consciousness plausibly exists in only a rudimentary form. While I have agreed with Godfrey-Smith in his assessment of the exclusive presence of evaluative experience in gastropods, I have argued against his suggestion of the exclusive presence of sensory experience in insects. Evaluation, as the pathological complexity thesis maintains, may indeed be at the core of consciousness—though we should also recognize that the animals existing in the here and now are not necessarily representative of the earliest sentient beings that may have had even more rudimentary forms of hedonic evaluation than gastropods that have had millions of years to fine-tune this capacity.

Finally, the arguments here should importantly not be misunderstood as definite proofs. My goal was not to make anything like a final assessment of the subjective experience of arthropods and gastropods, but rather to revive the comparative spirit of Griffin's cognitive ethology, in order to use functionalist reasoning about what kinds of subjective experience would make sense given the different life history strategies of different animals. The motivation of the pathological complexity thesis to seek the origins of consciousness in evaluation may well turn out to be ultimately misguided. But if we want to develop a true biological science of consciousness, we must begin with a firm understanding of the healthy lifestyles of different species in the normal natural environments they have evolved in. Only then can we answer the functionalist question of what consciousness is *for*, which can in turn help us to answer the question of what kinds of conscious experiences would be *worth having*. In asking for the possibility of sensory consciousness, or rather the extent of the subjective worlds of animals, we should ask which kinds of felt discriminations of distinct stimuli are useful for the kinds of evaluative activities a species is engaged in during its life cycle. The pathological complexity thesis offers us a framework to at least make some progress on these difficult problems by using the Darwinian lens of state-based behavioral and life history theory, which could, for instance, lend itself towards making predictions about color vision in species such as bees that are routinely engaged in economic trade-off calculations in their foraging activities. Within the scope of this article, I have restricted myself to fairly general thinking

about sensory and evaluative experience in gastropods and arthropods, but future work will inevitably take a much more narrow and precise approach focusing on particular species in order to make predictions that could in turn be tested and corroborate the framework presented here.

Unfortunately, the importance of evolutionary thinking has so far been neglected in a science that was hard-pressed by the behaviorist *Zeitgeist* to make itself seem as objective as possible (Birch et al. 2022). But the time has come to draw on the greatest strength a Darwinian approach to biological phenomena has to offer: the comparative method. If nothing else, the pathological complexity thesis provides an evolutionary framework for just such a bottom-up comparative study of animal consciousness that might also enable us to solve the problem of interspecies comparisons of subjective welfare by providing something like a “sentience-multiplier” (see Browning 2022 a, b). I hope that this article has shown that a biologically well-informed understanding of the diverse life history strategies we find in nature can and should play an important role in discussions of animal consciousness. Overcoming the resistance to such an approach may allow us to—in Griffin’s words—write the final, crowning chapter of the Darwinian revolution.

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## Declarations

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## References

- Adamo SA (2016) Do insects feel pain? A question at the intersection of animal behaviour, philosophy and robotics. *Anim Behav* 118:75–79
- Allen C, Bekoff M (1997) *Species of mind: the philosophy and biology of cognitive ethology*. MIT Press, Cambridge
- Allen C, Fuchs PN, Shriver A, Wilson HD (2005) Deciphering animal pain. In: Aydede M (ed) *Pain: new essays on its nature and the methodology of its study*. MIT Press, Cambridge, pp 351–366
- Appel M, Elwood RW (2009) Motivational trade-offs and potential pain experience in hermit crabs. *Appl Anim Behav Sci* 119(12):120–124
- Barron AB, Klein C (2016) What insects can tell us about the origins of consciousness. *Proc Natl Acad Sci USA* 113(18), 4900–4908
- Bateson M, Desire S, Gartside SE, Wright GA (2011) Agitated honeybees exhibit pessimistic cognitive biases. *Curr Biol* 21(12):1070–1073
- Birch J, Schnell AK, Clayton NS (2020) Dimensions of animal consciousness. *Trends Cogn Sci* 24(10):789–801
- Birch J, Broom DM, Browning H, Crump A, Ginsburg S, Halina M et al (2022) How should we study animal consciousness scientifically? *J Conscious Stud* 29(3–4):8–28
- Birch J, Burn C, Schnell A, Browning H, Crump A (2021) Review of the evidence of sentience in cephalopod molluscs and decapod crustaceans. Department for Environment, Food and Rural Affairs, London
- Blackstone NW (2001) Crustacea (crustaceans). eLS. <https://doi.org/10.1002/9780470015902.a0001606.pub3>
- Browning H (2017) Anecdotes can be evidence too. *Anim Sentience* 16(13). <https://doi.org/10.51291/2377-7478.1246>
- Browning H (2019a) What is good for an octopus? *Animal Sentience*. 26(7)
- Browning H (2019b) What should we do about sheep? The role of intelligence in welfare considerations. *Animal Sentience* 25(23)
- Browning H (2020) If I could talk to the animals: measuring subjective animal welfare. PhD thesis, Australian National University. <https://doi.org/10.25911/5f1572fb1b5be>
- Browning H (2021) Assessing measures of animal welfare. Preprint. <https://philsci-archive.pitt.edu/17144/>
- Browning H (2022a) The measurability of subjective animal welfare. *J Conscious Stud* 29(3–4):150–179
- Browning H (2022b) The problem of interspecies welfare comparisons. Preprint. <http://philsci-archive.pitt.edu/20115/>
- Browning H, Birch J (2022) Animal sentience. *Philosophy Compass*. e12822: 1–14
- Browning H, W (2020a) Improving invertebrate welfare. *Animal Sentience* 29(4). <https://doi.org/10.51291/2377-7478.1585>
- Browning H, Veit W (2020b) The measurement problem of consciousness. *Philosophical Top* 48(1):85–108
- Browning H, Veit W (2021) Evolutionary biology meets consciousness: essay review of Simona Ginsburg and Eva Jablonka’s *The Evolution of the Sensitive Soul*. *Biology & Philosophy* 36(5)
- Browning H, Veit W (2022) The sentience shift in animal research. *The New Bioethics*. <https://doi.org/10.1080/20502877.2022.2077681>
- Budd GE, Telford MJ (2009) The origin and evolution of arthropods. *Nature* 457(7231):812–817
- Carew TJ, Walters ET, Kandel ER (1981) Associative learning in *Aplysia*: cellular correlates supporting a conditioned fear hypothesis. *Science* 211(4481):501–504
- Colwill RM, Absher RA, Roberts M (1988) Context-US learning in *Aplysia californica*. *J Neurosci* 8(12):4434–4439
- Crook RJ, Walters ET (2011) Nociceptive behavior and physiology of molluscs: animal welfare implications. *ILAR J* 52(2):185–195

- Crump A, Browning H, Schnell A, Burn C, Birch J (2022) Sentience in decapod crustaceans: a general framework and review of the evidence. *Anim Sentience* 32(1). <https://doi.org/10.51291/2377-7478.1691>
- Dennett D (2019) Review of *Other Minds: the octopus, the sea and the deep origins of consciousness*. *Biol Philos* 34:2
- Eisemann C, Jorgensen W, Merritt D, Rice M, Cribb B, Webb P, Zalucki M (1984) Do insects feel pain? A biological view. *Experientia* 40(2):164–167
- Elwood RW (2012) Evidence for pain in decapod crustaceans. *Anim Welf* 21(S2):23–27
- Feinberg T, Mallatt J (2016) *The ancient origins of consciousness*. MIT Press, Cambridge
- Gibbons M, Versace E, Crump A, Baran B, Chittka L (2022) Motivational trade-offs in bumblebees. *bioRxiv*. <https://doi.org/10.1101/2022.02.04.479111>
- Ginsburg S, Jablonka E (2019) *The evolution of the sensitive soul: learning and the origins of consciousness*. MIT Press, Cambridge
- Godfrey-Smith P (2020a) *Metazoa: animal minds and the birth of consciousness*. Harper Collins UK, London
- Godfrey-Smith P (2020b) Varieties of subjectivity. *Philos Sci* 87(5):1150–1159
- Griffin DR (1998) From cognition to consciousness. *Anim Cogn* 1(1):3–16
- Groening J, Venini D, Srinivasan MV (2017) In search of evidence for the experience of pain in honeybees: a self-administration study. *Sci Rep* 7(1):1–8
- Hentschel E, Penzlin H (1982) Beeinflussung des Putzverhaltens bei *Periplaneta americana* (L.) durch Wundsetzung, Naloxon-, Morphin- und Met-Enkephalingaben. *Zoologische Jahrbücher Abteilung für allgemeine Zoologie und Physiologie der Tiere* 86:361–370
- Jacquet J, Franks B, Pungor J, Mather J, Godfrey-Smith P, Marino L et al (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*, pp 1–30
- Labandeira CC (2006) Silurian to Triassic plant and insect clades and their associations: new data, a review, and interpretations. *Arthropod Syst Phylogeny* 64:53–94
- Maruzzo D, Bortolin F (2013) Arthropod regeneration. In: Minelli A, Boxshall G, Fusco G (eds) *Arthropod biology and evolution*. Springer Berlin, Heidelberg, pp 149–169
- Mather JA (2008) Cephalopod consciousness: behavioural evidence. *Conscious Cogn* 17(1):37–48
- Misof B, Liu S, Meusemann K, Peters RS, Donath A, Mayer C et al (2014) Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346(6210):763–767
- Mitoh S, Yusa Y (2021) Extreme autotomy and whole-body regeneration in photosynthetic sea slugs. *Curr Biol* 31(5):R233–R234
- Perry CJ, Baciadonna L, Chittka L (2016) Unexpected rewards induce dopamine-dependent positive emotion-like state changes in bumblebees. *Science* 353(6307):1529–1531
- Schnell A, Browning H, Birch J (2022) Octopus farms raise huge animal welfare concerns—and they’re unsustainable too. *The Conversation*. <https://theconversation.com/octopus-farms-raise-huge-animal-welfare-concerns-and-theyre-unsustainable-too-179134>. Accessed 4 July 2022
- Schwartz SK, Wagner WE Jr, Hebets EA (2016) Males can benefit from sexual cannibalism facilitated by self-sacrifice. *Curr Biol* 26(20):2794–2799
- Smith JM (1952) The importance of the nervous system in the evolution of animal flight. *Evolution* 6(1):127–129
- Sprecher SG, Cardona A, Hartenstein V (2011) The *Drosophila* larval visual system: high-resolution analysis of a simple visual neuropil. *Dev Biol* 358(1):33–43
- Suzuki Y, Chou J, Garvey SL, Wang VR, Yanes KO (2019) Evolution and regulation of limb regeneration in arthropods. In: Tworzydło W, Bilinski S (eds) *Evo-devo: Non-model species in cell and developmental biology. Results and problems in cell differentiation*, vol 68. Springer, Cham, 419–454. [https://doi.org/10.1007/978-3-030-23459-1\\_17](https://doi.org/10.1007/978-3-030-23459-1_17)
- Tye M (2016) *Tense bees and shell-shocked crabs: are animals conscious?* Oxford University Press, Oxford
- Veit W (2021) Biological normativity: a new hope for naturalism? *Med Health Care Philos*. <https://doi.org/10.1007/s11019-020-09993-w>
- Veit W (2022a) Complexity and the evolution of consciousness. *Biol Theory* (in press)
- Veit W (2022b) Consciousness, complexity, and evolution. *Behavioral and Brain Sciences* 45, e61. <https://doi.org/10.1017/S0140525X21001825>
- Veit W (2022c) Health, agency, and the evolution of consciousness. PhD thesis, University of Sydney. Manuscript in preparation
- Veit W (2022d) A philosophy for the science of animal consciousness. Book manuscript in preparation
- Veit W (2022e) Review of Peter Godfrey-Smith’s *Metazoa: Animal Minds and the Birth of Consciousness*. *Philos Sci*. <https://doi.org/10.1017/psa.2022.26>
- Veit W (2022f) The origins of consciousness or the war of the five dimensions. *Biol Theory* (in press)
- Veit W, Browning H (2022) Pathological complexity and the evolution of sex differences. *Behavioral and Brain Sciences* (in press). Preprint: <http://philsci-archive.pitt.edu/20237/>
- Veit W, Harnad S (2020) 4 years of animal sentience. *Psychology Today*. <https://www.psychologytoday.com/blog/science-and-philosophy/202003/4-years-animal-sentience>. Accessed 4 July 2022
- Veit W, Huebner B (2020) Drawing the boundaries of animal sentience. *Animal Sentience* 29(13)
- Veit W, Ney M (2021) Metaphors in arts and science. *Eur J Philos Sci* 11(44). <https://doi.org/10.1007/s13194-021-00351-y>
- Veit W, Rowan AN (2020) The rising concern for animal welfare. *Psychology Today*. <https://www.psychologytoday.com/au/blog/science-and-philosophy/202003/the-rising-concern-animal-welfare>. Accessed 4 July 2022
- Walters ET (2018) Nociceptive biology of molluscs and arthropods: evolutionary clues about functions and mechanisms potentially related to pain. *Front Physiol* 9:1049
- Walters ET, Carew TJ, Kandel ER (1981) Associative learning in *Aplysia*: evidence for conditioned fear in an invertebrate. *Science* 211(4481):504–506
- Wigglesworth VB (1980) Do insects feel pain? *Antenna* 4:8–9
- Zuk M (2016) Mates with benefits: when and how sexual cannibalism is adaptive. *Curr Biol* 26(23):R1230–R1232