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INSTRUCTIONS FOR COMMENTATORS

Minds without spines: Evolutionarily inclusive animal ethics

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Abstract: Invertebrate animals are frequently lumped into a single category and denied welfare protections despite their considerable cognitive, behavioral, and evolutionary diversity. Some ethical and policy inroads have been made for cephalopod molluscs and crustaceans, but the vast majority of arthropods, including the insects, remain excluded from moral consideration. We argue that this exclusion is unwarranted given the existing evidence. Anachronistic readings of evolution, which view invertebrates as lower in the *scala naturae*, continue to influence public policy and common morality. The assumption that small brains are unlikely to support cognition or sentience likewise persists, despite growing evidence that arthropods have converged on cognitive functions comparable to those found in vertebrates. The exclusion of invertebrates is also motivated by cognitive-affective biases that covertly influence moral judgment, as well as a flawed balancing of scientific uncertainty against moral risk. All these factors shape moral attitudes toward basal vertebrates too, but they are particularly acute in the arthropod context. Moral consistency dictates that the same standards of evidence and risk management that justify policy protections for vertebrates also support extending moral consideration to certain invertebrates. Moving beyond a vertebrate-centered conception of welfare can also clarify foundational moral concepts in their own right.

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1. Introduction

Even though they are remarkably diverse behaviorally, cognitively, and evolutionarily, invertebrate animals are often lumped into a single category and excluded from welfare-based consideration. Where invertebrates are given ethical consideration in the regulation of research and in common morality, it is largely limited to considerations of conservation, where their value is assessed instrumentally in terms of the ecological services they provide within broader communities and ecosystems (Eisenhauer et al. 2019; Sánchez-Bayo & Wyckhuys 2019). Although the ecological approach to moral value makes sense for insentient animals (such as corals), it is inadequate for invertebrates with brains that could support rich forms of cognition and sentience, and thus a psychological welfare of their own. Major scientific funding agencies, such as the National Institutes of Health (NIH), request information about proposed use only concerning vertebrate animals, explicitly encouraging scientists to replace vertebrates with invertebrates to promote ethically sounder research (Wilson-Sanders 2011, p. 127). Recently, some regulatory bodies in the European Union and Institutional Animal Care and Use Committees in the United States have created an exception for cephalopod molluscs (coleoids [octopuses/squid/cuttlefish] + nautiloids), which have attained the status of 'honorary vertebrates' as their cognitive capacities have drawn widespread recognition (Directive 2010/63/EU 2010; Low et al. 2012). U.S. federal agencies, however, such as the USDA, continue to classify cephalopods along with all other invertebrates as mere 'dissected tissue' (Carere & Mather 2019).

Although these protections for coleoid cephalopod molluscs are encouraging, other invertebrate lineages with centralized nervous systems and flexible behaviors, such as arthropods (insects/crustaceans + arachnids + myriapods), continue to receive little to no welfare consideration even though they have been the subject of a systematic and wide-ranging empirical investigation indicating that they have mental capacities that could give rise to morally protectable interests. Prompted by Elwood's (2011; see also Harvey-Clark 2011) research and lobbying, the EU did recently consider (though it ultimately rejected) granting protections to decapod crustaceans. We are aware of no such proposals for other arthropod groups, such as insects and spiders, which comprise the vast majority of arthropods found in nature and used in laboratories.

Much of the prevailing ethical thought on invertebrates took hold during a time when little was known about the cognitive capacities, neurological complexities, and flexible behaviors of certain invertebrate species. Over the last several decades, however, a growing body of research is pointing to sophisticated cognitive abilities in a number of invertebrate lineages. There is growing evidence that some molluscs and arthropods have the capacity for subjective experience (i.e., *sentience*: Klein & Barron 2016; Mather 2019a; Godfrey-Smith 2017). Nevertheless, with rare exceptions, such as the recent attention afforded to octopuses (Godfrey-Smith 2016), philosophers and policymakers have continued to operate on the basis of outdated information about invertebrate cognition and behavior. Philosophers who have engaged with invertebrate cognition and consciousness (e.g., Schwitzgebel 2018; Klein & Barron 2016; Feinberg & Mallatt 2016/2018; Tye 2016) have typically demurred on the ethical implications of these findings. (One exception is Carruthers (2007), whose view is discussed in §3.3, has taken a stance but a negative one.) Philosophical discussions of animal welfare, meanwhile, have focused on mammals and birds, extending only recently to basal vertebrates like fishes (see the commentary on Woodruff 2017). Although pioneering work on invertebrate welfare is found in scientific forums (see ILAR 2011; Carere & Mather 2019),

it has interacted little with philosophical ethics and has been met with resistance in public policy — although there are signs this landscape is beginning to change (Rethink Priorities 2019).

In this target article, we argue that the exclusion of certain invertebrates from bioethics and science policy is not warranted given the state of the evidence and plausible conceptions of moral standing. We attribute the exclusion of arthropods in general, and terrestrial arthropods in particular, to the following four factors:

(i) a lingering progressivist reading of evolution according to which invertebrates are lower in the *scala naturae*;
(ii) the *a priori* assumption that small brains are unlikely to support sophisticated cognition or sentience (which is contrary to the existing body of behavioral and neuroscientific evidence, principles of evolutionary continuity, and the potential for convergence on psychological functions);
(iii) human cognitive-affective biases that distort moral judgments and mental state attributions concerning unfamiliar, disgust-provoking beings;
(iv) an inappropriate balancing of scientific uncertainty and moral risk.

Although some or all of these problems are likely to shape moral attitudes and policy toward basal vertebrate lineages (such as fish and lizards), they are particularly acute in the arthropod context. Similarly, while uncertainties about the presence of sophisticated forms of cognition and sentience pervade all of comparative cognitive science, they are most pronounced in research on the minds of invertebrates, whose brains, behaviors, and life histories share few ancestral similarities with those of vertebrates. Appreciating the diverse forms of sentience found throughout the animal kingdom may not only lead to a more inclusive animal ethics, but it may also shed light on foundational moral concepts themselves. Making progress on these issues, however, requires that we engage with the formidable conceptual and methodological challenges that confront the scientific and moral study of 'alien' minds on Earth.

2. Challenging the Invertebrate Dogma

To understand the differential ethical treatment that has been accorded to vertebrates and invertebrates, it is useful to begin with the problematic nature of the distinction itself. The category 'invertebrate' does not represent a proper clade, since the groups included under this umbrella do not share a single common ancestor that is not also shared with vertebrates. Moreover, the vertebrate-invertebrate distinction lumps the immense diversity of invertebrate life into a single undifferentiated category, doing more to obscure morally relevant cognitive diversity among animals than to illuminate it. Worse still, the vertebrate-invertebrate dichotomy is a value-laden one, with invertebrates taken, either explicitly or implicitly, to occupy a lower rung in the *scala naturae*. Pre-Darwinian evolutionary iconography, such as Ernst Haeckel's Pedigree of Man, depicts the history of life as an 'ascent' from monad to man with invertebrates occupying the second-lowest tier, just above protozoa but below non-mammalian vertebrates.

Whereas biology has long since jettisoned progressivist readings of evolutionary history, bioethics and policy remain very much encumbered by them. For instance, The NIH asks researchers who are proposing to use vertebrates in an experiment to explain why 'less highly evolved' animal models, such as invertebrates, could not be used instead. We are not

suggesting that this anachronistic evolutionary baggage fully explains the moral exclusion of invertebrates. Nor does it show that this treatment of invertebrates is indefensible in principle. However, in raising suspicions about the validity of attitudes and institutionalized practices toward invertebrates, it provides a launching point for a fuller explanation and evaluation.

The most plausible justification for the moral exclusion of invertebrates is that they lack the psychological properties that give rise to 'moral standing,' or the intrinsic value that places constraints on how a being may be treated. There is no consensus about the minimum psychological conditions necessary for a life that matters for its own sake (Buchanan 2009). Nor is there agreement about the psychological conditions above this minimum that give rise to higher moral statuses or, if one prefers, to weightier moral interests. There is, however, broad philosophical consensus that to have a welfare is to have a life that can go well or poorly for the subject of experience. What makes a life go well or poorly can be glossed in different ways, such as in terms of pleasure and pain, the fulfillment of desires, the pursuit of valuable personal projects, an 'objective' list of circumstances that would make one's life go well irrespective of one's actual desires, and so forth (Crisp 2017). At the center of all of these views, however, is an experiencing subject of a life that matters in its own right. If invertebrates do not have welfares, then they have no interests, preferences, or desires to take into account and hence they may be exploited as mere instruments to the ends of others. For these reasons, we operate on the assumption that welfare is a psychological property and that some form of mental life is a precondition for morally protectable interests. Some more expansive theories of moral standing would include entities whose insentience is uncontroversial, such as bacteria, forests, and rivers, but we will not address those views here (see Basl 2019 for a critical discussion).

We will refer to the notion that invertebrates are not loci of welfare — and hence that they may be excluded from ethical consideration in research, husbandry, agriculture, and human activities more broadly — as the 'invertebrate dogma.' In what follows, we will argue that the current state of comparative research on brains, behavior, consciousness, and emotion suggests that even small-brained invertebrates are likely to have welfares and hence moral standing. Many of the same experimental paradigms that have been used to establish the existence of sophisticated cognition and sentience in vertebrates have also been used — and their findings replicated — in research on invertebrate cognition. The case we will make, therefore, is one of consistency: the same empirical and philosophical basis for extending protections to all vertebrates calls for extending similar protections to some invertebrate clades.

2.1 Brains. One reason invertebrates with complex brains and behavior may be thought to lack the cognitive and affective properties that comprise a welfare is the high prior probability some assign to the notion that very small brains cannot (or are highly unlikely to) generate mental states. The idea is that there are minimum neuro-computational thresholds for mind that are not met by invertebrates. This is not a concern in the case of some coleoid molluscs, such as octopuses, whose neural densities and structural complexities rival those of mammals (even taking into account the distributed nature of coleoid nervous systems). However, the same cannot be said for other, small-brained invertebrates, such as arthropods, who comprise a large fraction of invertebrates used in research. The assumption that small brains are unlikely to support sentient life is problematic, however, for several reasons.

First, the neuro-computational thresholds needed to generate minimum mental capacities are unknown and cannot be determined from the armchair. Neural network analysis is helpful insofar as it allows us to experiment with minimal wiring solutions for specific cognitive functions, but these are highly idealized; independent evidence is needed to establish that the options selected by the model would have been available to natural selection. It is critical, therefore, that we investigate what small centralized nervous systems can actually do in the world. Just as important, we need to work out how they do these things (see Budaev et al. 2019 for further discussion). Behavioral data from carefully controlled experiments are indispensable for both these projects. Until we have a fully worked out and empirically corroborated theory of the relationships among neural tissue, cognitive processes, and phenomenology, we are not in a position to rule out or even deem unlikely the possibility that tiny brains can give rise to sentient lives with interests that merit moral protection.

Second, relative brain size is a better indicator of cognitive sophistication than absolute brain size, since (ceteris paribus) it indicates that there has been differential evolutionary investment in metabolically costly brain tissue that pays for itself through the cognitive functions that additional neuro-processing power provides. However, even relative brain-size analysis is too coarse-grained (Healy & Rowe 2006), especially across distantly related taxa (Logan et al. 2018), to allow for any definitive judgments about cognitive potential. More fine-grained features, such as total neuron number, neuron density, connectivity, metabolic rate, and modularity are better indicators of the cognitive capacities of brains (Chittka & Niven 2009; Chitkka & Farris 2012). Most of these features, however, do not scale linearly with size. A higher neuron number, for instance, might be achieved by increasing not brain volume but neuron density, and by shrinking the size of neurons (Olkowicz et al. 2016).[1] Although arthropods have smaller neuron totals than coleoids and vertebrates, neural network models suggest that some forms of cognition may be computationally inexpensive and can be accomplished with small numbers of neurons (Logan et al. 2018). As with computers, bigger is not necessarily better. There is no reason to think that there are high minimum size thresholds for the presence of the kinds of mental states that factor into sentience.

More important than total computing power is how information is integrated in the brain and embodied in the organism, as inferred from the structure of brains and behavior. The brains of many insects, spiders, and coleoid molluscs have structural characteristics that could support sophisticated forms of cognition. In particular, they have central processing regions (the 'mushroom bodies' and central complex in arthropods and the vertical lobes in coleoids) that continuously receive, integrate, and exchange information with peripheral systems via 'reentrant pathways' (Giurfa 2013; Edelman & Gally 2013), permitting centralized coordination of multi-modal sensory information and executive (top-down)

[1] Smaller brain size may actually confer advantages. For example, smaller brains tend to have shorter inter-neuronal distances; these shrink the distance that information has to travel and thus conduction delays. Arthropods also have multi-functional neurons that economize on available space and energy while preserving a range of functionalities. At the same time, miniaturization may force tradeoffs, such as between modularity (needed for functional specialization) and redundancy (needed for parallel processing). Miniaturization also imposes costs: for example, it restricts total neuron number and limits available energy by reducing space for mitochondria. (For comprehensive reviews, see Chittka & Niven 2009 and Niven & Farris 2012.)

control. The cognitive signatures of centralized information processing are reflected in the behavioral complexity of these animals, as we shall now see.

2.2 Behavior and cognition. Although some researchers were initially skeptical that flexible behaviors could be generated by tiny arthropod brains, the combined weight of the neuroscientific and behavioral evidence suggests that complex cognition may be much more broadly distributed in the tree of animal life than previously thought. It is now well known that coleoid molluscs (octopus, squid, and cuttlefish), who have large, hierarchically structured brains, have excellent spatial navigation and communication abilities, excel at problem-solving, and may even use rudimentary tools (Mather 2019a; Finn et al. 2009). Less widely appreciated is the substantial accumulation of experimental evidence, thanks in large part to the pioneering work of Lars Chittka and his collaborators, that some arthropods are capable of sophisticated cognitive feats that indicate the presence of a richer mental life than traditionally thought, one that may give rise to a welfare.

For example, among the insects, there is evidence that honeybees can learn abstract concepts (Chittka 2017; Howard et al. 2017) including same/different, larger/smaller, and above/below. They can also transfer these concepts across sensory modalities (e.g., from vision to olfaction). Honeybees can be taught addition and subtraction procedures (Howard et al. 2018/2019), appear to have the concept of 'zero' (Nieder 2018), and can learn to attend to global or local features of objects (Dyer et al. 2016). Bumblebees can not only learn complex and highly non-instinctive tasks, such as rolling a tiny ball (Loukola et al. 2017) or pulling a string to reel in a reward: they can transmit this information culturally (Alem et al. 2016). They can also recognize objects and patterns through one modality (e.g., touch, olfaction) that they previously encountered only in another modality (e.g., vision) (Solvi et al. 2020; Lawson et al. 2018). Bees and wasps can recognize human faces, although only wasps do so without prior training (Dyer et al. 2005; Chittka 2017). One study suggests that ants can pass the mirror self-recognition test (Cammaerts 2015), which human infants only pass at around 20 months of age. There is even tantalizing evidence of causal reasoning and means-end rationality in bees (Loukola et al. 2017) and transitive inference in paper wasps (Tibbetts et al. 2019).

Bees are excellent models for the study of invertebrate cognition because they are highly trainable, responsive to rewards, and neurologically complex. For these reasons, while bees may be model insects, they are not necessarily the best model *for other* insects. The extent to which findings in bees (or hymenopterans more broadly) generalize to other arthropods is unclear. However, flexible learning mechanisms and the neural correlates of attention have also been shown in flies, cockroaches, and other insect orders (for a review, see Greenspan & Swinderen 2004). Among arachnids, jumping spiders (salticids) have been shown to plan routes that include elaborate detours, deploy sophisticated ambush strategies, and switch flexibly among hunting techniques in order to overcome the defenses of unfamiliar prey types (Harland & Jackson 2000). Salticids have also demonstrated numerosity abilities at the level of human infants (Cross & Jackson 2017); many insects seem to have such capacities (Skorupski et al. 2018; Giurfa 2019). These findings are consistent with 'thinking' broadly construed and, taken in conjunction with comparative brain data, call the invertebrate dogma into question.

Many of the arthropod cognition studies are modelled on studies of vertebrate cognition, which were adapted from paradigms in human developmental psychology.

Although performance is not always comparable across invertebrate and vertebrate animals (see Abramson & Wells 2018 for examples and discussion), experiments that do show parallel results are instructive: Bees have been taught to distinguish between human painting styles (such as impressionism and cubism) using techniques and controls that were used to demonstrate the same ability in pigeons (Wu et al. 2013). Bees and wasps can learn to recognize faces and patterns holistically (Avarguès-Weber et al. 2010), with performance that approximates that of vertebrates trained to make the same sorts of discriminations (Marzluff et al. 2010). Bees were found to respond to ambiguous stimuli with decreased confidence and to opt out of difficult choices (Perry & Barron 2013) using the same uncertainty-monitoring paradigm that has been used to probe for this aspect of metacognition in a wide variety of vertebrates, from rats to dolphins (Foote & Crystal 2007; Smith & Washburn 2005). Tests of numerosity in jumping spiders use the same 'looking time' paradigm — measuring surprise and expectation — that is used to probe for belief-states in vertebrates including pre-linguistic humans. Honeybees were found to discriminate quantities containing up to six items on a delayed match-to-sample task (Gross et al. 2009), the same task that has been used productively with vertebrates such as dolphins and rhesus macaques (Killian et al. 2003; Brannon et al. 2000). Studies of affect in bees and flies use the same 'cognitive bias' paradigm as in studies of emotion in vertebrates (Mendl et al. 2009; more on this in §2.3).

The same behavior can have multiple cognitive realizations, so these findings might reflect evolutionary convergence on behavioral flexibility without convergence on the underlying cognitive mechanisms that produce that flexibility. Deflationary (simpler) cognitive explanations of impressive arthropod performance cannot be decisively ruled out. (On association-based explanations of abstract concept learning in insects, see Vasas & Chittka 2019; Cope et al. 2018.) However, and this is key, neither can deflationary cognitive explanations of vertebrate performance be ruled out, even in the case of very young human children. Moreover, complex cognitive explanations of invertebrate behavior may turn out to be less burdensome computationally and more parsimonious — and in these respects 'simpler' (see §4.1) — evolutionarily than their deflationary counterparts (Perry & Chittka 2019). Thus, in the absence of other assumptions that have yet to be articulated, the behavioral evidence does not justify the asymmetrical ethical treatment of vertebrates and invertebrates.

That said, it is not clear that the cognitive capacities probed in the above experiments are necessary conditions for moral standing, since creatures may be sentient even if they lack, say, numerosity, transitive inference, or problem-solving. Nor are these cognitive abilities clearly sufficient for moral standing: a system may be capable of sophisticated cognitive feats but lack the feeling that would ordinarily accompany them, as may be true of some AI and insentient robots. Nevertheless, these findings do point to the ability to classify the world into meaningful categories, to forge new associations among them, and to make these available for adaptive action. Such flexible learning abilities are probably underwritten, at least in naturally evolved organisms, by valenced states of pleasure and pain that motivate learned discriminations and configure sentient experience.

2.3 Sentience. The traditional idea that arthropods are incapable of flexible learning and do not form sophisticated representations of their world has been refuted by the body of research on invertebrate cognition summarized above. Nevertheless, one could try to salvage

the invertebrate dogma by arguing that even if small-brained invertebrates like arthropods are surprisingly sophisticated cognitively, they lack the felt experience and emotional capacities that make them matter morally.

2.3.1. Subjective experience. If a creature is incapable of experience — if there is nothing it *feels like* from the inside to be that creature (Nagel 1974) — then it cannot be a locus of pleasurable and aversive states, it has no interests that can be set back, and hence it can be neither harmed nor benefitted. In other words, there is no meaningful notion of psychological welfare for that system. Phenomenal consciousness is thus a precondition for moral standing (Kahane & Savulescu 2009).

Phenomenal consciousness was traditionally linked to human-like cortical structures, and hence it was widely assumed that animals who lack these structures (e.g., fishes, birds, and all invertebrates) are unlikely to be subjects of experience (Key 2016; Rose 2002). However, there are several clear limitations of this homology-based approach. First and most obviously, it overlooks the possibility that there has been evolutionary convergence on the neurofunctional organizations that give rise to experiencing subjects (Dinets 2016; Elwood 2016; Güntürkün 2012, Güntürkün & Bugnyar 2016; Low et al. 2012). Second, many cortical functions in humans were co-opted from more ancient brain structures that predated the evolution of the cortex. Third, the cortex-centric approach does not explain why vertebrates that lack the six-layered cortex found in mammals (such as birds, lizards, and fish) are commonly included in the research ethics calculus, whereas invertebrates are systematically excluded.

Furthermore, complex functional traits (sensory, locomotive, computational, metabolic, etc.) can not only be realized by disparate anatomical, developmental, and biomolecular bases — they are also generally continuous rather than discrete. Thus, one might expect phenomenal consciousness to be continuously distributed in the animal world with no clear cut-off between experiencers and those that are incapable of experience. The key unanswered question, of course, is what the lowest bounds of this spectrum might look like. On the other hand, some theorists (e.g., Carruthers 2019) contend that phenomenal consciousness is a discrete rather than continuous property: the lights are either on or off; there is no 'dimmer switch.' But even if the capacity for experience does not admit of degrees, this, too, leaves the minimal experience problem unresolved: how we identify the simplest or most primitive character states that give rise to conscious experience.

It has also been shown, however, that many cognitive and perceptual functions are carried out unconsciously in humans (for a review, see Boly et al. 2013). This decoupling has led some ethologists (Cartmill 2017) and philosophers (Allen-Hermanson 2008) to suggest that arthropods may be the closest that evolution has come to producing real-life examples of 'philosophical zombies' (Chalmers 1996) — logically conceivable creatures whose behavior is indistinguishable from that of conscious beings but for whom all is 'dark on the inside.' This case is strengthened by robots that replicate the behavior of nonhuman animals without, presumably, reproducing the experiential qualities that are normally thought to attend those behaviors. However, there is a large gap between the idea that some cognitive operations and behaviors are carried out unconsciously in humans or human artifacts and the notion that active, intentional, behaviorally flexible, and yet wholly non-conscious cognitive creatures actually exist in the world.

Alternatively, one might accept that some invertebrates are phenomenally conscious but deny they are moral patients on the grounds that they do not exceed the 'richness' threshold for the content of subjective experience that is necessary for moral standing (see, e.g., Frey 1983). No one has yet demonstrated precisely what such a threshold would look like, however, nor on what philosophical grounds it would be justified. Moreover, if arthropod behavioral experiments probe the cognitive content of conscious experience, then there is evidence for cognitively 'rich' experience in arthropods of the sort often used to justify extending protections to vertebrate animals in research and agricultural contexts.[2]

2.3.2. Feeling. Phenomenal consciousness alone is not an adequate basis by which to establish the existence of a welfare. It is empirically inadequate because the concept of phenomenal consciousness is hotly contested and, on some definitions, impossible to measure. It is conceptually inadequate because, in addition to having experiences, a being must also *care* about what happens to it in some basic sense. And if things are to matter to an organism, it must be capable of experiencing states of affairs as pleasurable or aversive, even if it does not explicitly recognize them as such. We think this affective glossing of conscious experience is better captured by the term *sentience*.[3]

Unlike phenomenal consciousness, whose causal powers and evolutionary functions are unclear, affectively valenced states play a clearer role in adaptive behavior. The motivational force of emotions comes from the embodied feelings that attend a given appraisal (James 1890). Without the ability to attach feelings to actions and objects, animals (at least as they are constituted on Earth) would be incapable of complex action, decision-making, and learning (Damasio 1994). Some arthropods appear capable not only of perceiving objects as 'bound' wholes rather than non-integrated collections of local features, but capable also of classifying objects into appropriately valenced categories like 'predator,' 'prey,' 'mate,' 'foraging item,' 'obstacle,' etc., which in turn support sophisticated feats of learning, navigation, foraging, and cooperation.

The scientific study of affect among invertebrates is still fairly new, but evidence suggests that insects have convergently evolved 'emotion-like' states or embodied action tendencies that in some cases are mediated by the same neurotransmitters that modulate emotion in humans (Perry et al. 2016; Burke et al. 2012: see Baracchi et al. 2017 for careful review). For example, bumblebees tend to interpret ambiguous stimuli more optimistically after exposure to a pleasant stimulus, just as humans tend to do when they are happy or calm. Conversely, vigorously shaking bees appears to induce a pessimistic bias in odor discrimination tests. In these experiments, bees are first trained to associate one odor with a

[2] There is an ongoing philosophical debate over how to think about the relation between cognitive sophistication and moral considerability. Some understand moral considerability in terms of differences in moral statuses that are achieved when a certain threshold of mental capacity is met (such as sentience or rationality); others would describe moral considerability in terms of a single threshold for sentience beyond which there is a continuum of interests that are factors in different moral obligations (for discussions, see DeGrazia 2008; McMahan 2009). Our argument is compatible with both of these approaches.

[3] Whether the presence of affect is an indicator of phenomenal consciousness depends on the theories of affect and consciousness that one chooses to adopt; it also depends on whether one conceives of valence in representational terms or rather as an intrinsic quality of evaluative experience (Carruthers 2018). If valence is an intrinsic quality of experience, then all phenomenally-conscious states are sentient states and all phenomenally-conscious creatures are sentient creatures.

sucrose reward and another with quinine punishment, and then they are presented with samples containing different ratios of each odor (Bateson et al. 2011). While Bateson et al. interpreted their results as indicating that bees have emotion-like states, Giurfa (2013) advanced an alternative deflationary explanation, which was subsequently cited favorably in a major review of pain in animals (Sneddon et al. 2014). According to Giurfa's interpretation, the shaking may have triggered improved discrimination rather than inducing displeasure. However, if shaking had improved judgment, then shaken bees' performance should have improved for all discriminations, including ambiguous odors toward the sucrose-rich (pleasant) end of the spectrum. Instead, Bateson's results show a steady decline in the shaken bees' willingness to sample any of the options, exactly as the pessimism hypothesis predicts.

2.3.3. Pain. Of all affectively valenced feelings, pain is perhaps most at the center of moral questions surrounding the treatment of nonhuman animals. The evidence for vertebrate-like pain in invertebrates is mixed and inconclusive. Many invertebrates have nociceptors, or specialized neural receptors that detect tissue damage. These specialized cells predate the split of bilaterally symmetric animals into deuterostomes (vertebrates and echinoderms) and protostomes (all other bilaterian invertebrates), and are hence present in bilaterians without centralized nervous systems (Smith & Lewin 2009). If we presume that pain perception requires a brain, then nociception is not sufficient for pain perception (Allen et al. 2005). While there is agreement that pain perception occurs downstream of nociceptor input (Tracey 2017), the nature of that downstream processing remains poorly understood.

Markers of traditional pain perception include the presence of endogenous opioids, responsiveness to anaesthetics and analgesics, grooming of injured body parts, a reduction in grooming behavior under analgesia, and 'motivational tradeoffs' such as when hermit crabs are willing to withstand a mild electric shock in order to obtain a more desirable shell (Elwood 2011/2012). Shrimps groom their antennae after sustaining an injury — a behavior reduced when given an analgesic (Barr et al. 2008). Coleoid molluscs show long-term nociceptive sensitization following moderate injury (Crooke et al. 2011), and a recent study showed that anaesthetic agents commonly used in research with octopuses and cuttlefish do not merely immobilize them, but actively suppress both afferent and efferent signals to and from the CNS, suggesting that these agents suppress not only nociception but also pain perception (Butler-Struben et al. 2018). On the other hand, some insects engage in normal feeding and mating behaviors even after sustaining severe injuries, such as dismemberment (Eisemann et al. 1984; Smith 1991). If confirmed, these findings would suggest either that these animals do not experience pain (Broom 2013), that they do not experience pain in the way that vertebrates do,[4] or that the circumstances generating pain in these lineages differ from those in vertebrates.

[4] There is also no reason to think that pain is more likely to have attendant subjective states than other cognitive and affective states. If we assume that unconscious affective states are possible, as some representationalist theories of mind allow (Carruthers 2019), pain 'zombies' may be just as conceivable as cognitively complex zombies. Although some would contend that pain is necessarily *painful*, research on a condition known as *pain asymbolia* calls this into question. Subjects with this condition report experiencing pain *as pain* but not as unpleasant or aversive, which suggests that the perception of pain and the experience of its aversiveness can come apart. There is some controversy over whether individuals with pain asymbolia actually experience pain as affectively neutral or whether they are simply indifferent to and unmotivated by

Even if cognitively sophisticated invertebrates do not experience pain *in the same way* that mammals and other vertebrates do, this would not imply they have no morally protectable interests. A being may have a rich phenomenal and affective inner life, and hence a welfare of its own, even if it lacks vertebrate-like experiences in response to tissue damage. It is important to distinguish pain perception narrowly understood from a broader notion of suffering that includes stress, frustration, and other aversive states that flow from the inability to fulfill one's desires. The presence or absence of vertebrate-like pain response is relevant to the question of what sorts of treatments are ethically permissible, but it should not be the focal point in our conception of moral standing. Nor are our moral obligations limited to providing environments that are free of pain broadly construed; they also require that we provide positive conditions in which sentient animals can flourish — environments in which they can experience greater amounts of pleasure and develop their natural range of abilities (Nussbaum 2009).

There are sound theoretical reasons to think that arthropods and some other invertebrates are capable of experiencing pleasurable and aversive states. The leading evolutionary explanation of pain is that pain facilitates instrumental learning, helping animals to avoid future exposure to dangerous or noxious agents. If pain is an adaptive mechanism through which animals learn which situations to avoid — and pleasure the same in reverse — then an animal that is capable of instrumental learning may also be capable of experiencing aversive and pleasurable states (Godfrey-Smith 2017). The presence of open-ended associative learning in a lineage — including the ability to attach valences to non-stereotypical action sequences — is thus potentially a useful indicator of sentience (Ginsburg & Jablonka 2019). As we have seen, there is evidence that some invertebrates, such as some molluscs and insects, are capable of instrumental learning. This is supported by the large body of research on invertebrate cognition discussed above, as well as experimental evidence of learning via negative reinforcement (Tedjakumala & Giurfa 2013; for a survey of associative learning in invertebrates, see Hawkins & Byrne 2015).

At the same time, however, there are reasons to be skeptical about arthropod pain. In their highly cited review of the animal pain literature, Sneddon et al. (2014) argue that the success of robotic models in simulating some aspects of pain behavior undercuts the case for pain in arthropods (see also Adamo 2016). Their reasoning is that pain behavior can be reproduced by systems that are clearly incapable of experiencing pain, and thus 'insects, and possibly other animals, could use simple processing rules to produce pain-like behaviour, without any internal experience of pain' (Sneddon et al. 2014). They go even further to suggest that there is currently no definitive evidence that insects have the cognitive and emotional capacities that could support aversive mental states.

But why single out insects in this regard? Indeed, one of the robotic models they cite is a robotic 'rodent' designed to reproduce vertebrate-like pain behavior. If robotic models drive a wedge between behavioural evidence and ascriptions of pain perception, they ought to do so for all animals — vertebrates included. Moreover, the requirement that evidence of pain perception be 'definitive' is at odds with prevailing evidentiary standards for any proposition in the field of comparative cognition, let alone for policies that are intended to

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the experience of pain (Klein 2015). In any case, as with unconscious cognition, the fact that pain states in a subset of humans with a dysfunctional condition are not experienced as painful does not establish that some sentient creatures are in fact pain-zombies.

manage moral risk (see §4). Zombie hypotheses cannot be definitively ruled out; but this is as true for vertebrates, including other humans, as it is for invertebrates.

3. Cognitive-Affective Biases

Lingering progressivist readings of evolution (see Chapman & Huffman 2018) and dismissive views about the mental capacities of invertebrates are probably not the whole story behind the treatment of invertebrates. Historically, the pernicious moral exclusion of human groups has resulted from cognitive-affective biases that shape empirical beliefs and judgments about moral standing (Buchanan & Powell 2018; Powell et al. 2020). We are in no way equating the moral exclusion of invertebrates with the mistreatment of human beings; our point is simply that the treatment of invertebrates in policy, philosophy, and common morality may offer another illustration of moral exclusion driven by these distorting influences.

3.1 The empathy gap. Empathy is well known to modulate moral judgment: people tend to morally favor those they empathize with over those with whom they do not. And people tend to empathize with individuals who look more like them, who are judged to be more aesthetically attractive, who are potential reciprocating partners, and who are classified as members of one's in-group. They tend to have less empathy for — and hence to pass more severe moral judgment upon or assign lower moral weight to — individuals who are less similar, less subjectively attractive, or belong to an out-group such as a disfavored race, ethnicity, or nationality (Prinz 2011; Hewstone 1990). Empathy also mediates attributions of mental states: empathy deficits are associated with dementalization (the wholesale denial of mind), decreased mentalization, and reduced sympathy for the victims of violence (for a review, see Kozak et al. 2006). At the same time, the 'cuteness response' (Sherman & Haidt 2011) — an emotional state directed at beings deemed to be cute — is associated with enhanced empathy and mental-state attribution and it increases prosocial engagement in ways that lead to moral inclusion.

The 'alien-ness' of invertebrate morphologies and lifeways makes the empathy gap difficult to bridge. The vast majority of invertebrates with complex brains, such as coleoid molluscs and many arthropods, are rarely considered attractive, cute, or cuddly, and their body plans, some of their behaviors, communications, forms of sociality, and life histories are very unfamiliar to humans. As a result, they do not tend to elicit empathy or to be accorded mental states; this in turn makes it more likely that their interests will be discounted in moral decision-making. There is also evidence that a timescale bias influences mind attribution: animals and robots that move at human-typical speeds are more likely to be attributed mental states than those that move at speeds unfamiliar to humans (Morewedge 2007) such as those typical for arthropods (fast) and molluscs (slow).

3.2 The disgust response. Perhaps more important than the lack of empathy-eliciting features in invertebrates is the outright disgust many of these animals trigger in a large fraction of the human population. The disgust reaction and associated 'gape face' is thought to have originally evolved as a mechanism for avoiding pathogens (Kelly 2011); however, disgust appears to have been co-opted to mediate social interactions and regulate moral judgment (Fischer 2016; Kumar 2017; May 2018). In modern humans, disgust plays an important role in driving morally exclusionary norms, attitudes, and behaviors. Using disgust to trigger dehumanization is a well-known tactic of would-be genocides and ethnic cleansers.

Nativist and racist propagandists draw explicitly on the disgust response toward nonhuman animals in portraying immigrants and other out-group races and ethnicities as disease-bearing vermin; insects like cockroaches, rats, or lice; or free-riding social parasites 'leeching' off the hard work of the 'pure' races (for reviews, see Haslam 2006; Navarrete & Fessler 2006). Whereas the cuteness response promotes increased social engagement with subjectively cute beings, disgust leads to avoidance and disengagement from disgust-eliciting beings (Sherman & Haidt 2011). Disgust can cause people to fail to attribute (or to under-attribute) not only intentional cognitive states but also experiential qualities such as pain perception (Waytz et al. 2010), leading to 'moral disengagement' (Bandura 2002).

If invertebrates — especially arthropods like insects and spiders — score very low on the empathy scale, they receive high marks on the scale of subjective disgust. Priming for disgust increases the moral derogation of human agents (Schnall et al. 2008; Eskine et al. 2011), and we might expect it to operate similarly, if not more acutely, when directed at beings who are the immediate objects of the disgust response. Many arthropods map generically onto ecological categories that are associated either with parasite threat or physical dangers such as stings and bites, even though few of them actually pose a threat to humans. A number of arthropod parasites prey directly on humans, and larval forms of certain insects are associated with rotting flesh, dung, and other disgust-triggering stimuli. Although these account for a small fraction of arthropods, they tend to provoke an overgeneralized aggression-avoidance response that is characteristic of antisocial attitudes under conditions of perceived parasite threat (Fincher & Thornhill 2012; Navarrete & Fessler 2006). Although negative attitudes toward invertebrates are to some degree culturally transmitted and ameliorated by exposure and education (Mather 2019b; Shipley et al. 2017), they are likely to emanate in part from an entrenched adaptive heuristic for managing risk in the Pleistocene and perhaps earlier in vertebrate-arthropod coevolution. It should not be surprising, therefore, that disgust-provoking animals like arthropods tend to be excluded from any institutionalized morality that relies on empathetic response.

3.3 Moral justification. In one of the rare substantive philosophical discussions of arthropod moral standing, philosopher of mind Peter Carruthers (2007) argues that although some arthropods are probably capable of having beliefs and desires that give rise to interests, we have no reason to care about their welfare and hence to afford them ethical protections:

> *It is a fixed point for me that invertebrates make no direct claims on us, despite possessing minds in the sense that makes sympathy and moral concern possible. Invertebrates believe things, want things, and make simple plans, and they are capable of having their plans thwarted and their desires frustrated. But it isn't wrong to take no account of their suffering. Indeed, I would regard the contrary belief as a serious moral perversion.* (p. 296)

Carruthers maintains, in effect, that invertebrates pose a 'slippery slope' problem for animal ethics: Either we must extend moral consideration to arthropods — which he takes to be patently absurd — or else we must reject welfarist accounts of animal moral standing in favor of some alternative account, such as a contractualist view which would limit moral standing to rational agents who can make and respond to moral claims.

If Carruthers's argument were sound, it would remove nearly all nonhuman animals, vertebrates included, from moral consideration. It would not, therefore, single out

invertebrates for special exclusion, despite their being the central focus of his article. As we see it, the rhetorical role that invertebrate welfare plays in Carruthers's argument is to show that the welfarist approach to moral standing leads to an absurd conclusion: namely, that we ought to care about the wellbeing of some invertebrates. However, this begs the very question at issue by simply asserting that extending moral consideration to some invertebrates is patently absurd — an intuition that Carruthers takes as 'a fixed point,' rather than one that is subject to critical revision in light of new empirical evidence or philosophical argument. Why should we reject a coherent, well-worked out, and highly corroborated theory of moral standing, rather than scrutinize a moral intuition that supposedly conflicts with it? Indeed, we should be suspicious of moral intuitions when there is reason to think they have been distorted by cognitive-affective biases (Clarke & Roache 2009), which, as we've seen, are especially pronounced in the arthropod context.

Although Carruthers does not subscribe to a rank speciesism or 'phyla-ism,' his view is fundamentally at odds with prevailing 'subject-centered' accounts of where moral obligations come from (Buchanan & Powell 2018). On these views, intrinsic moral worth is grounded not in an individual's contingent ability to care about or cooperate with beings of a particular sort, but rather in that individual's possession of certain morally relevant psychological properties. And there is wide agreement, not only among Utilitarians but also among contemporary Kantians (e.g., Korsgaard 2018), that it is sentience — not the capacity for reason — that sets the minimum bar for being a member of the moral community.

Carruthers also worries that the moral inclusion of invertebrates would require humans to sweep the floor before them like Jainist Monks, so as to avoid stepping on scurrying ants and beetles, to say nothing of changes to the global agricultural industry which relies heavily on pest management — a ridiculous requirement, he believes, for any secular morality. The concern that 'moral standing creep' could result in overly demanding restrictions on valuable human activities has also figured in the literature on fish welfare (e.g., Key 2016). There are several problems with this 'overdemandingness' objection as it relates to invertebrate inclusion. First, the fact that living up to our moral obligations is hard is a patently inadequate reason for failing to meet those obligations.

Second, the over-demanding line wrongly assumes that moral standing confers equally robust protections on all who have it. The fact that an individual meets the minimum threshold for moral *standing* does not entitle that individual to equal treatment (Singer 1974; DeGrazia 2008) or confer on them equal moral *status* (Buchanan 2009). Beings with different moral statuses may have different sets of rights, and some moral statuses may be accorded no 'rights' at all (conceived in terms of their inviolability) even if they entail interests that constrain the behavior of moral agents. Similarly, on a continuum of interests view, some types of interest (such as future-directed ones) may outweigh others when they come into conflict, which is frequently how experimentation on sentient beings who lack future-directed interests is justified (within the bounds of unnecessary suffering). Thus, even if some invertebrates have interests that are in conflict with our own, resolving these conflicts should take the same form as conflict-resolutions between humans and non-rational vertebrates in moral triage scenarios. Whether harm to a small number of vertebrate subjects is morally preferable to harm to a large number of invertebrate subjects is unclear. But such questions should be resolved through an analysis of interest conflicts, not by according some legitimate interests no weight at all.

Third, some apparent interest conflicts may disappear once we realize that what counts as a harm to human persons may not be a harm to many sentient animals. For example, while a painless death is a harm to persons because (e.g.) it frustrates their interest in a valuable future, death may not be a harm to animals who have no such future-directed interests (McMahan 2002). Thus, including some invertebrates in the moral community may not require that we shoulder unpalatable moral burdens, such as drastically altering our lifeways or the modes and fruits of scientific enterprise (but see Sebo 2018).

4. Managing Uncertainty in Science and Ethics

Thus far, we have argued that the evidence does not justify the asymmetrical treatment accorded to vertebrates and invertebrates, and we have suggested that a number of questionable empirical assumptions combined with cognitive-affective biases created this inconsistent state of affairs. We do not mean to give the impression that there are no significant uncertainties concerning the mental capacities of invertebrates. In this section, we will consider these scientific uncertainties and how they should interact with ethical science policy.

4.1 Error avoidance in comparative cognition. One general problem facing comparative cognitive science is that competing explanations often cannot be adjudicated through behavioral evidence alone. The field has typically responded to this 'underdetermination' challenge by adopting a policy of erring on the side of avoiding false positives: ascribing sophisticated mental states to animals who do not in fact have them. This methodological strategy is based on the assumption that, all else being equal, one should prefer the simplest hypothesis consistent with the evidence, where 'simplest' is typically taken to mean 'least cognitively sophisticated' (Shettleworth 2010; Heyes 2012). Simpler explanations can almost always be given, though, and where one fails, another will often rise to take its place. The preference for simplicity may be especially strong in the invertebrate context, where it is likely to interact with aspects of the invertebrate dogma, such as the belief that small brains are unlikely to generate sophisticated cognition. For example, some are likely to interpret the fact that bees replicate findings of cognitive research on mammals and birds not as evidence for the presence of sophisticated cognition in invertebrates, but as a reason to think that the underlying experiments are flawed or that the cognitive capacities being tested are simpler than typically thought — either in bees or generally in nonhuman animals. This conclusion is bolstered by the fact that, as noted earlier, simple neural networks and robots can recreate aspects of invertebrate behavior.

There is now a substantial literature arguing that the preference for simplicity is conceptually problematic, empirically unsubstantiated, and likely to lead comparative cognitive science away from rather than toward the truth (Mikhalevich et al. 2017; Mikhalevich 2015; see also Sober 1998; Fitzpatrick 2016; Dacey 2016). Because this problem applies to all of comparative cognition, we will not delve into it here. However, it is worth noting that some of the inferential strategies that might help resolve the underdetermination problem are inaccessible in the invertebrate research context. For example, one way of adjudicating competing cognitive hypotheses when they are underdetermined by behavioral observation is to bring other sources of evidence to bear on the adjudication, such as comparative brain data. If the *same* brain structures known to support complex cognition in

some animals are present in others due to their inheritance from a common ancestor, then this will add weight to the inference of sentience.

These homology-based strategies are generally not available in the invertebrate context, however. The centralized nervous systems of invertebrates exhibit little clear structural homology with vertebrates, since their brains evolved largely (or entirely) independently from vertebrates and from one another (for a discussion of the most likely nervous system structure of the last common bilaterian ancestor, see Ginsburg & Jablonka 2019; Powell 2020; Northcutt 2012; Erwin & Valentine 2011). Homologies at lower levels, such as cell-type and signaling molecules (deFur 2004), do not have any straightforward implications for sentience or cognitive sophistication. Therefore, if comparative brain data can be used to break the evidential impasse in the case of invertebrates, it will have to be mainly evidence of the functional, not historical, kind (Mikhalevich et al. 2017).

As we saw earlier, convergent brain macrostructures dedicated to central processing and integration appear to exist in some invertebrates and are corroborated by behavior elicited in experiments. Could the preferential treatment of vertebrates over invertebrates nevertheless be justified by the greater confidence that brain homology (similarity due to common descent) permits in ascribing sentience? There are several reasons to doubt this. First, without a well-worked out theory of sentience that tells us what sorts of functional configurations we should be looking for, we have no way of knowing what level of homology to target. If we take healthy adult humans as the prototypical case of sentience: we cannot know how phylogenetically deep the inference of homology should go (e.g., to all primates, mammals, tetrapods, vertebrates, etc.) unless we have already identified the structures in humans that give rise to sentience. Once we have done so, we can determine the distribution of those same characteristics in vertebrates more broadly. The trouble is that homologies must be delineated in part by their similarities in function, whether these are cashed out in terms of the causal (Amundson & Lauder 1994) or evolutionarily selected (Rosenberg & Neander 2009) roles they perform. In other words, homology hypotheses are used to explain and classify characters that have already been individuated using various functional metrics; if this is so, then homology hypotheses are not function-free and hence have no distinct advantages over functional analyses of convergent brains.

4.2 Error-avoidance in ethics and science policy. One effect of the simplicity preference in comparative cognition is that it results in a bias toward false negatives, or failing to attribute sentience and sophisticated cognition when in fact they are present. Whether or not the preference for false negatives is justified in this domain of research, in bioethical policy there are reasons to take the opposite approach: that is, to err on the side of avoiding false negatives, or scenarios in which we fail to identify a morally relevant cognitive property in nonhuman animals or margin-zone humans when they actually possess them. If the costs of falsely attributing sentience to animals are minor while the costs of false negatives are high (because, for instance, they result in a great deal of unnecessary suffering), then erring on the side of false positives is prima facie ethically preferable. How should we manage the moral risk that flows from scientific uncertainty about invertebrate welfares?

Ethicists and policy-makers often appeal to the 'precautionary principle' (PP), which on standard accounts holds that we need not await scientific certainty before taking precautionary measures to avoid harm to health or the environment (Sneddon et al. 2014). While this may sound like a reasonable approach, there is significant disagreement over how

the PP should be formulated, whether it is conceptually coherent, whether it is addressed to a regulatory straw man, and whether it provides concrete, rational guidance on matters of practical moral concern (Sunstein 2003; Powell 2010; Steele 2013). Birch (2017) proposes a version of PP that is specifically tailored to the animal welfare context, which he calls the Animal Sentience Precautionary Principle (ASPP). According to the ASPP, 'where there are threats of serious, negative animal welfare outcomes, lack of full scientific certainty as to the sentience of the animals in question shall not be used as a reason for postponing cost-effective measures to prevent those outcomes' (Birch 2017, p. 3).

Birch's account has two major virtues. The first is that it attempts to specify the relevant evidential threshold below scientific certainty at which precautionary measures should kick in. For Birch, the evidential bar for ethics and policy should be set at statistically significant and scientifically valid evidence of 'at least one credible indicator of sentience' in at least one species of an order, which may then be generalized to other species of that order. The second virtue relates to Birch's proposed decision procedure, which is designed to kick in once a credible indicator of sentience is found. According to ASPP, rather than leading to irrational moral paralysis, wherever the epistemic criterion is met, animal subjects must be included in ethical regulatory regimes, but experimental research on those subjects can continue so long as minimal welfare requirements are met.

Birch's analysis is a marked improvement over the traditionally vague language of precaution, but we believe it could be strengthened on several points. First, Birch cites pragmatic justifications for generalizing to the entire Linnaean order: it is not feasible to test all species of an order for sentience, he argues, and thus we may generalize from a single credible indicator of sentience in a single species to the entire order in which that species belongs. Although Birch does not state it explicitly, this justification can only be partly practical — the other part must be theoretical, grounded in a two-fold hypothesis about homology: first, that the last common ancestor of the 'order' (more accurately, the order-level clade) was sentient, and second, that the conservation of sentience is more likely than its loss in a given order. Both these assumptions need to be defended. The trouble is that the 'polarity' of a character (i.e., whether it is ancestral or derived) cannot be ascertained without examining how that character is distributed in a clade, which is precisely the problem at issue here and which Birch claims cannot feasibly be assessed. This point can be illustrated by applying the ASPP to language: The ASPP would have us infer from the fact that humans have language that all primates (including not only apes, but also monkeys and lemurs) have this trait. Yet there is overwhelming evidence that the last common primate ancestor — a shrew-like creature that branched off from other mammalian orders not long after the end-Cretaceous extinction — did not have so much as the rudiments of language, and thus the inference based on order-level homology is not justified. Other phylogenetic problems with the ASPP that stem from its anachronistic Linnaean formulation are discussed by Brown (2017) and Mallatt (2017).

Second, even if the strategy of inferring homology could be salvaged, the generalization only kicks in if a morally relevant mental capacity can be reliably attributed to at least one taxon within a given order. The problem is that some will reject the claim that a 'credible indicator of sentience' has been shown in cases where cognitive hypotheses are underdetermined by the behavioral evidence. It is not immediately obvious how the ASPP would (or should) handle cases of behavioral underdetermination, though one approach would be to factor in extra-experimental evidence (such as comparative brain data) and to

err moderately on the side of over-attribution in light of the biases discussed above and given the moral costs of getting it wrong. In addition, although Birch is operating with an appropriately broad notion of sentience that includes positive and aversive states, his analysis focuses almost entirely on traditional pain perception, which leaves him agnostic on the question of invertebrate (especially arthropod) moral standing. We have already seen the limits of pain-centered approaches, such as their failure to extend moral protections to beings with rich inner worlds that lack traditional markers of pain perception. We have also suggested that although pain perception may be a sufficient condition for moral standing, a broader range of cognitive and affective abilities should bear on the determination of sentience (see §3). The search for a credible indicator of sentience should avail itself of the full breadth of evidence, including not only behavioral experiments but also ecology, neuroscience, and evolutionary biology; it should also probe for markers of sentience that go beyond familiar expressions of pain in response to tissue damage. All told, however, the precautionary spirit of Birch's account could remain valid even if his generalization strategy were abandoned in favor of a broader evidence-based approach.

Finally, there is a normative problem with Birch's discussion that it shares with much of the PP literature. Namely, it pays inadequate attention to the moral costs that could flow from acting out of precaution. Given the high costs of false negatives and the impracticalities of testing for sentience throughout the animal kingdom, why not simply generalize to all bilaterian animals, rather than (as Birch recommends) to all taxa within a given order? The answer, presumably, is that overgeneralization has moral costs. If these costs are likely to be substantial — for instance, because erring on the side of caution would significantly interfere with or constrain research designed to benefit humans or other sentient animals — then aspiring to more targeted judgments about the presence of morally relevant cognitive properties may be ethically preferable. If so, then we have strong moral incentives to get the attribution of sentience right; extreme positions that require either very high or very low levels of certainty ought to be rejected.

5. Summary and Conclusion

We have argued that the nearly wholesale exclusion of invertebrates with central nervous systems from bioethics and science policy is not justified by the current state of the evidence. This exclusion is likely driven in part by outdated evolutionary ideas, stereotypes about the rigid instinctual behaviors of small-brained animals, cognitive biases that distort moral attitudes toward these deeply unfamiliar creatures, and flawed strategies for managing scientific and moral uncertainty. We have not offered any practical recommendations for changing the treatment of invertebrates. (For concrete policy proposals regarding a range of invertebrates, including arthropods, see Carere & Mather 2019; Rethink Priorities 2018; Crooke 2013; Horvath et al. 2013; and Cooper 2011.) Our goal here has not been to determine whether invertebrates can suffer under specific experimental conditions or live well in others; rather, we addressed a more foundational question: whether these animals are capable of suffering or flourishing at all. We have made a case for consistency in moral treatment: the same kinds of data and reasoning that justify moral protections for vertebrates favor extending similar protections to *some* invertebrates. Invertebrate brains comprise upwards of 99% of the brains that exist on Earth. Cognitive theorists have begun to appreciate the intellectual rewards of studying invertebrate cognition and sentience. It is time that ethicists and policy makers do the same.

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