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## The evolutionary history of consciousness

Commentary on [Klein & Barron](#) on *Insect Experience*

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**Abstract:** Klein & Barron argue that insects are capable of subjective experience, i.e., sentience. Whereas we mostly agree with the conclusion of their arguments, we think there is an even more important message to be learned from their work. The line of reasoning opened by Klein & Barron proves instructive for how neuroscientists can and should explore the biological phenomenon of consciousness.

**Keywords:** Arthropoda, Bilateria, cephalisation, invertebrate neurobiology, LUCSA, Nephrozoa, sensory integration, Urbilateria, Xenacoelomorpha

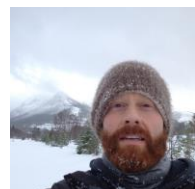
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## **1. Scientific Approaches to Consciousness**

Consciousness, once thought to be supernatural and unique to humans, is now known, undoubtedly, to be the product of animal evolution. This means that consciousness, even as experienced by humans, is the result of gradual modification of pre-existing traits. The only possible conclusion from this is that the animals around us possess various forms of consciousness that primarily differ from ours by degree. Unless we resort to supernatural explanations, this is indisputable.

It is, however, very contentious to what degree different animals are conscious, i.e., how they experience their world. The only animal for which we can say anything with certainty is humans (but see “the problem of other minds,” Hyslop, 2016). This has led to extensive arguments about the machinery, biological or otherwise, required for consciousness. This discussion has primarily been limited to mammals (Seth, Baars, and Edelman, 2005) and other vertebrates (Cabanac, Cabanac, and Parent, 2009; Feinberg and Mallatt, 2013). The consequence of this restriction has been that most researchers have assumed invertebrates to be void of consciousness, something akin to how we imagine a thermostat experiencing regulating temperature.

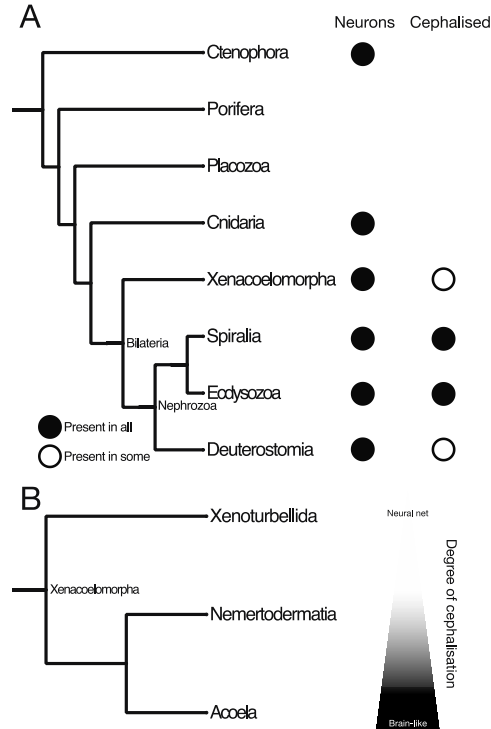
## **2. Consciousness in Invertebrate Animals**

In the philosophy of consciousness, sentience is the ability to feel (anything at all) subjectively. Klein & Barron (K & B) refer to this as subjective experience (Barron & Klein, 2016; Klein & Barron, 2016) and have rejected the notion of “simple” invertebrates, setting forth the claim that insects are capable of sentience. Although this claim may seem radical, K & B’s assessment is relatively straightforward and makes intuitive sense, from both a biological and an evolutionary perspective. More important, in our view, their papers clearly attempt to define the requirement for sentience: a rudimentary sense of space. K & B do not mean just the ability to move through the environment and respond to external stimuli (e.g., a robot tracking a light source), but rather centralised integration of motor output and sensory input. This allows an organism to keep track of how it moves through space and how space (and the elements within that space) moves around it. K & B argue that having this somato-spatial capacity is necessary/sufficient for sentience. Here we avoid delving deeper into this claim and instead attempt to see where such a naturalistic hypothesis of sentience can take us.

## **3. The Evolution of Consciousness and LUCSA**

This simple claim leads to a few predictions about sentience that make it possible to start the arduous work of tracing its evolutionary origins and history. A centralised nervous system (CNS) capable of integrating sensory information and motor output is required. Sentience can therefore not have emerged prior to nervous system cephalisation, and sentience cannot exist outside of Bilateria (Fig. 1A), as this is the only place we find CNS. The pattern of cephalisation observed in Xenacoelomorpha (Gavilan et al., 2015) makes it unlikely that Urbilateria, the

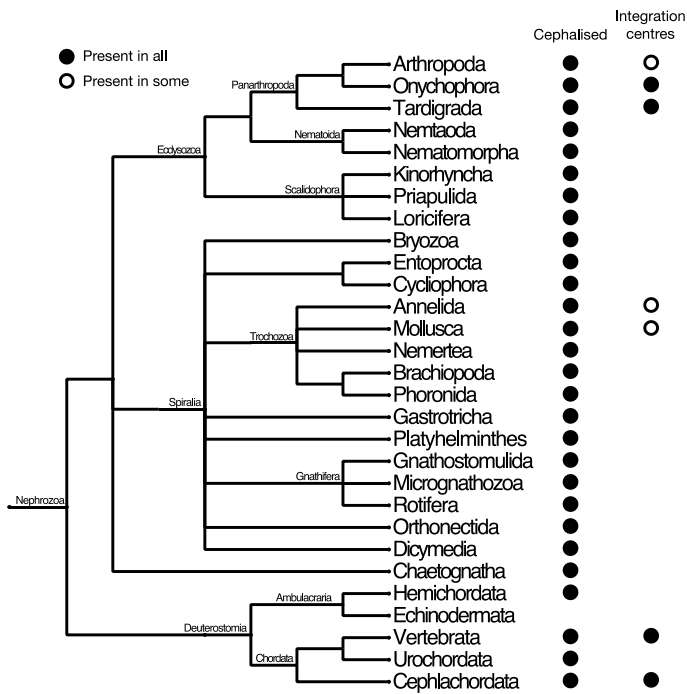
ancestor of all bilateral animals, was sentient (Fig. 1B). Within Nephrozoa we find cephalisation in all major branches (Fig. 1A), so it could have originated prior to the split between these groups.



**Figure 1.** (A) The only place in nature we find animals with centralised nervous systems is within Bilateria. Phylogeny based on Dunn, Giribet, Edgecombe, and Hejnol (2014). (B) It is unlikely that centralised nervous systems evolved before Xenacoelomorpha and Nephrozoa split because Xenoturbellida have only epidermal nerve nets. It is also unlikely that sentience evolved independently within Acoela because their nervous system appears incapable of the kind of integration hypothesized. Phylogeny based on Cannon et al. (2016).

We are thus left with two interesting scenarios: sentience predates the division of proto- and deuterostomes, or it evolved independently multiple times. K & B briefly mention the former scenario, drawing on a recent article by Strausfeld and Hirth (2013), who argue that morphological and transcriptomic similarities between arthropod and vertebrate core control systems result from a common ancient origin. This is indeed a very tantalising hypothesis; it means that the ancestor of all nephrozoan animals was sentient. This ancestor, the Last Universal Common Sentient Ancestor (LUCSA), must, at a minimum, have had a nervous system with a higher brain centre, perhaps similar to the insect central complex. To determine whether the LUCSA hypothesis is correct, many hurdles still need to be cleared. There are rival explanations of why higher brain regions in disparate animals appear similar; we, like others (e.g., Farris, 2015), believe that the current evidence points more strongly towards homoplasy than conservation.

The LUCSA hypothesis suggests some interesting conjectures, for example, that sentience originated only once and has been lost numerous times. K & B mention how nematodes lack the machinery for sentience, but LUCSA suggests that this was not because their lifestyle never necessitated it, but because it was lost. Nematodes are just one example among many, as most nephrozoan phyla do not have integration centres (Fig. 2).



**Figure 2.** With the exception of Echinodermata, all animal phyla within Nephrozoa have centralised nervous systems. However, only a few groups have the dense neuropils that may be required for the integration of sensory input and motor output that gives animals a sense of space. Phylogeny after Dunn et al. (2014).

Of course, we do not yet know what kind of neural machinery is required for the kind of integration envisioned by K & B. Nor do we have a functional characterisation of the existing circuitry within most of these phyla. To move forward with this question it might be instructive to investigate what has occurred at the family, genus, and species levels. For example, among the insects we have many examples of species that have gone through extreme miniaturization, discarding the majority of their brain (sometimes even dispensing with the nucleus of their neurons, Polilov, 2012). By studying the neural circuitry of these insects, it might be possible to determine whether they retained the same functional integration despite severely reduced neural tissue. A basic wiring-plan across all of Nephrozoa comprising a very limited number of neurons that allow for sentience would make LUCSA a lot more plausible.

#### 4. The Future of Consciousness Research

This may all sound like idle speculation at this point, and we completely agree, but it opens an important door. We are certain that if we want to understand consciousness, we must take a scientific approach and resolve the evolutionary history of this trait. We thus have two very important tasks ahead of us: (1) we must try to come to terms empirically with what kinds of “cognitive machinery” are necessary to support sentience, and (2) we must investigate widely across animal phyla, including amongst the invertebrates, to determine where they are present.

On a final note, if the K & B predictions should be wrong, and, say, temporal integration is what matters (Engel and Singer, 2001), it will of course change specific statements above, but the overall point remains: consciousness is accessible to a naturalistic understanding.

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