DOI: 10.1017/psa.2026.10274

This is a manuscript accepted for publication in *Philosophy of Science*.

This version may be subject to change during the production process.

The 21st Century Mind-Body Problem

Carrie Figdor

University of Iowa, carrie-figdor@uiowa.edu

Abstract: This paper articulates how recent advances in comparative behavioral and biological research are changing the nature of the mind/body problem from a human mind/human body problem to a problem of conceptualizing and organizing diverse types of minds in a hierarchical relational structure that is non-contingently related to phylogeny. It also discusses the impact of this refinement on our assessments of modal claims about possible artificial (AI) consciousness.

1. Introduction.

Advances in comparative behavioral and biological research are motivating significant scientific and philosophical attention to the evolution of mind. This paper fills a gap in this growing literature by articulating how these advances change the nature of the mind/body problem. In slogan form, the problem long conceived as "Mind and Its Place in Nature" (Broad 1925/2014) is is now that of "Minds and Their Places in Phylogeny". Where formerly the human mind – including but not limited to human conscious experience – was the only or primary subject, the human mind now falls within the subject of the hierarchical relational structure of many minds.

In what follows, I'll introduce the new mind/body problem in terms of the questions of how the diversity (or differentiation) and distribution of types of minds in phylogeny are related to the diversity and distribution of types of body. I'll describe the conceptual, metaphysical, and epistemological adjustments these questions require of physicalism, and illustrate the new problem using the ability to learn by association as a case study. I'll also sketch how this new problem affects approaches to the relation between consciousness and biological and nonbiological minds.

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

2. Minds, Mind Lineages, and Physicalism

Almost all of what we know about the evolution of life is the evolution of "body". In terms of (metaphorically vertical) levels of biological organization, "body" ranges from the molecular to the ecological: from RNA and DNA sequences, morphological structures, and developmental sequences to lifestyles in distinct physical and social environments. In terms of (metaphorically horizontal) relationships, it includes the lineages of parts and properties at each of the body levels – particularly genetics and morphology – that are used to create the nested hierarchies of clades, or groups of species comprising a common ancestor and all and only its descendants, that are displayed in phylogenies.

These lineages of parts and properties are more specifically relationships between characters.[1] Characters are the explananda and explanantia in theorizing about patterns of evolutionary continuities at multiple levels of biological organization and across species boundaries. Biologists were led to introduce characters into their ontology because of findings of patterns in morphology and development across species but within clades (e.g. Alberch and Gale 1985). Such findings required a theoretical apparatus at a distinct level of abstraction over individual phenotypes from that of species-typical phenotypes (such as the human brain, which generalizes over individual human brains).

For example, the canine tooth character is the same in humans, dogs, and narwhals even though each species-typical canine tooth phenotype is different in form and function. As this case shows, the phenotypes that determine the same character need not look intuitively or obviously similar. This theoretical apparatus grounds the classification of human brains as a type of primate brain (Herculano Houzel 2012), and avian and mammalian brain structures as homologues, or characters shared due to inheritance from their last common ancestor (Jarvis et al. 2005). Characters also fill the main jobs of traditional natural kinds: for example, knowing that a newly tested species in a new clade shares a character with species in other clades prompts new predictions about its presence in other species in the new clade and new explanations for why the

[1] There are a number of different character concepts, but the central one that used in phylogenetic systematics or cladistics, the field that classifies species by their theorized evolutionary history (Wagner 2001). The original concept is credited to Owen (1848) and was given an evolutionary interpretation in Darwin's "unity of type" (1859/1993). Efforts to introduce the character concept and phylogenetic methods into psychology include Papini (2002) and Maclean et al. (2012); see Griffiths (1997) for its use in emotion theory and Figdor (2024) for a generalized account.

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

character is shared across these clades. Theories of character individuation, identity, and novelty are debated, but the need to theorize about evolutionary patterns across species is not.

The comparative research that prompts the new mind/body problem stems from recent findings of more behavioral flexibility and more advanced cognitive abilities in more species in many branches of phylogeny. [2] These accumulating results are a loud wake-up call in relation to our long history of treating mind as uniquely human. Given what we know about the evolution of body, they imply that the mind side of the mind/body equation also forms lineages and nested hierarchies of groups of different sizes comprising general abilities and specialized versions of them within clades. They pressure mind researchers to adopt the metaphysical framework of characters, homologies, and related concepts of phylogenetic systematics that body researchers have used and refined since the 19th century.

Lorenz and Tinbergen pioneered taking this approach with their view that behavior forms evolutionary lineages (Burkhardt 2005). Generalizing their view, the 21st century mind/body problem is to understand how mind characters are related to body characters and how the phylogeny of mind is related to the phylogeny of body. In morphology, the typical starting point for character individuation is samples from a number of different species; the metaphysical issue is to extract the relevant similarities for character definition (which may not be superficial or obvious). For mind, the metaphysical issue is the same, but because we start from one species, we must distinguish those features of human mental states or abilities relevant for character definition from the bells and whistles unique to the human phenotype. Whether or not there are mind characters that are shared across all organisms, the actual space of mind characters is likely to be as complex as that of body characters.

One general consequence of this reformulation is to further marginalize the use of human phenotypes as the standards for ascribing mental phenomena to nonhumans, depending on how similar the nonhumans are to the human exemplars. This comparative method is like using the human canine tooth to argue that wolves have teeth that are canine-like and narwals don't have canines at all. However, the change has fundamental metaphysical, semantic, and epistemological implications for physicalism in particular. Metaphysically, a need for mind characters requires physicalists to commit to a new level of abstraction over individual

[2] I leave open when we have crossed from the behavioral to the cognitive, nor do the goals of this paper depend on determining where that line (however fuzzy) might be drawn, assuming we want one (e.g. Allen 2017; Cisek 2019).

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

phenotypes in order to define traits suitable for articulating and explaining evolutionary continuities and discontinuities across minds. The character concept does not rule out autapomorphy – a character found in only one species or family – but autapomorphy is a significant evolutionary fact that must be established empirically and not by definition.

Semantically, physicalists must confront the tradition of defining psychological terms and concepts by reference to human phenotypes. For this reason, cognitive ontology – the revision of human-centered folk psychological concepts, based almost exclusively on human brain and psychological research (Poldrack and Yarkoni 2016; Khalidi 2023) – may be appropriate for refining concepts of human mind phenotypes. But the new mind/body problem requires concepts that refer to the mind characters that the (updated) human mind phenotypes determine. Fixation on human brains and psychology obscures the actual scope of the conceptual challenge. Adding a framework of mind characters will entail a need for disambiguation depending on whether a term is used to refer to a human mind phenotype or to a mind character that human minds may share with other species.

Epistemologically, physicalists must explicitly limit the scope of their claims of reduction or non-reduction and recognize the different types of justification required to support them. In philosophy of mind, species-specific reductions are usually considered in terms of reducing phenotypes to (eventually) genotypes (e.g. Kim 1972) – that is, they are within-species claims. Within the new mind/body problem, reductive claims across species are claims about reduction of characters. That means reductive claims will have broader or narrower scope depending which clades have the character, and they will require different sources of justification if they are shared due to their common ancestry (homology) or to common environmental pressures (homoplasy).

To illustrate, Papini (2024) argues (in the case of learning) that if there is homology at the cellular-molecular, neurochemical, neurobiological, and psychological levels of organization, then the character (e.g. a learning mechanism) should be judged homologous, and otherwise not. This sets a high bar: as Ereshefsky (2012) notes, there is often "hierarchical disconnect" between homologies at one biological level and those at another. So we may fully explain habituation in a protist by detailing the molecular mechanisms involved, and many of these molecular mechanisms may be highly conserved, but it does not follow that habituation in a mammal is reducible to the conserved molecular mechanisms. It does follow that habituation can no longer be defined as distinct from sensitization partly by reference to a central nervous system (Barron

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

et al 2015). Overall, the new mind/body problem makes it highly unlikely that global claims about reduction (or not) of mind to body will be justified, while less-than-global claims will not be Kim-style species-specific reductions unless a character is unique to a species.

3. Distribution, Diversity, and Mind/Body Relations

The reconceptualized mind/body problem generates many new research questions. What mind characters are there and how should we define them? Which different phenotypes might determine the same character, and why? When might a given character have appeared in evolution, how did it differentiate since then, and what is its current phylogenetic distribution? Answering these questions is a work in progress. We have a reasonable grip on defining human mind phenotypes (*modulo* cognitive ontology). We also have mind concepts defined so broadly that they don't rule out any organism (Lyon et al. 2021). This is like having concepts of Michelin-restaurant-dining and metabolism, with nothing in-between. Much work on specific mental abilities and complex behaviors is needed before we can relate mind characters and lineages to those of body.

In this section I will flesh out two of the new questions and illustrate how they are being addressed in the case of associative learning. (For space reasons a more complete discussion must await another opportunity.) These are the diversity (or differentiation) question of what different types of mind characters there are, and the distribution question of how they might be distributed in phylogeny. These questions (and their answers) are not wholly distinct. How we individuate the characters depends on which organisms we initially think have them, since the phenotypes of any species in the sample contribute to defining that character or those that may be subordinate or superordinate to it. However, for expository purposes the questions can be discussed separately. The case of associative learning also shows how thinking of the mind/body problem as the mind/brain problem, let alone the human mind/human brain problem, is obsolete.

Associative learning – customarily including classical and operant conditioning – has widely accepted instances throughout phylogeny, a widely accepted basic vocabulary, and a substantial background of theoretical and empirical research in human and comparative psychology. It is also foundational for more advanced cognitive abilities. In recent years its evidence base has spread vertically in terms of biological mechanisms and behavior, and

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

horizontally in terms of newly tested species in new clades. Importantly, this evidence is being organized in phylogenetic, not merely taxonomic, terms.

The Distribution Question: Where are minds? Historically, this wasn't even a question: humans had reason (*nous*) or "higher", "advanced", "sophisticated" psychological traits. The most well-known alternative answer is that all biological organisms have minds (Maturana and Varela 1991). Both answers are structurally simple: mind depends on one type of body, or on all types without differentiation. The truth is in-between, yet in a way that species-specific reductions can't capture. For that, the phylogenetic framework is needed.

For example, where in phylogeny did associative learning first appear and how it has radiated since then (Pontes et al. 2020)? Researchers are looking at animals with neural nets or nonstandard types of neurons (Jékely et al. 2015; Loy et al 2021; Moroz and Romanova 2021, 2022), and at fine-grained subtypes of associative learning, such as those that require interval timing, which is not phylogenetically widespread (Abramson and Wells 2018). For example, we know that *C. elegans*, with 302 neurons, can learn by association, but cannot do trace conditioning, where there is a temporal gap between the conditioned (CS) and unconditioned (US) stimulus. Sea anemone, which are cnidaria and have nerve nets, have classical conditioning but not operant conditioning (Cheng 2023). If box jellyfish (also cnidaria) can also learn by association (Bielecki et al 2023; but see Prados 2023), then at least simple forms of associative learning do not require a brain, although more sophisticated forms may (Ginsburg and Jablonka 2019: 341). If plants can learn by association (Gagliano et al 2016; but see Adelman 2018), then even simple associative learning would not require neurons. All this exploratory research into the distribution question also has implications for how we explain the mechanisms of learning, commonly thought to depend on strengthening synaptic connections.

The distribution question is also implicit in Ginsburg and Jablonka's (2010) proposal that associative learning is a contributing cause of the Cambrian explosion of bilaterian bodies and the colonization of new ecological niches. An obvious implication of their proposal is that the explosion of body types was accompanied by an explosion of mind types as well, starting from an evolutionarily ancient molecular learning toolkit (Ginsburg and Jablonka 2019: 312). The same question is paramount in other proposals for interpreting behavioral results in phylogenetic terms (e.g. Papini 2002; Cisek 2019; Van Duijn 2017; Coombs and Trestman (2025).

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

Social learning is also being explored in nonhumans. Social learning includes learning from another individual via processes such as imprinting, mimicry, and imitation. Song learning is a key example in this area (Chen and Wiens 2020; Jarvis 2019), along with findings of different cultures and cultural norms within populations, such as tool manufacture and use differences between chimpanzee troops (Whiten et al 2005) and social, cultural, and norm-guided behaviors long thought exclusively human (Ramsey 2013; Allen 2019; Westra et al. 2024). This research provides a growing empirical basis for theorizing about the distribution of social learning in phylogeny, as well as the relation between individual and social learning (Heyes 2018).

The Diversity Question: What minds are there? This question concerns individuating different mind characters – types and subtypes of learning, decision-making, communication, and so on – as well as their lineage (causal) relationships. For example, species differ in the temporal extent of habituation learning and the temporal interval between the CS and US that may prevent trace conditioning (Van Duijn op.cit.). Other differences include the amount of integration of different things learned and the number of new domains or cases to which what is learned can be extended. More fine-grained distinctions among individual learning types will capture the patterns of learning differences we are finding in different species and clades.

The signature testing approach in comparative psychology (Taylor et al. 2022) promises to help define this complex space of more or less fine-grained mind characters. This approach involves testing species to find patterns of biases, errors, limits, and so on across a number of different tasks, rather than seeing if they succeed in passing a particular test (such as a mirror self-recognition task). Signature testing may reveal that particular clades in phylogeny exhibit patterns of biases in learning that would help define a learning character characteristic of that clade. This approach would complement those arguing for a bottom-up approach, in which we look for cognitive "building blocks" and build up from there (de Waal and Ferrari 2010). In non-metaphorical terms, the latter approach aims to identify cognitive characters that are widely distributed or highly conserved across body lineages. In these terms, the diversity question is the problem of how exactly we build up from the bottom, without treating the human mind as the apex.

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

Discoveries of significant commonalities on the body side may help in this effort. Our increasingly fine-grained knowledge of body, both horizontally and vertically, can be leveraged to help define mind characters at multiple grain sizes. Investigation of neurotransmitters and other signaling molecules shows surprising homologies at cellular and molecular levels between animals and plants (Meyerowitz 2002). The establishment of brain homologies across animal clades provides supporting evidence for behavioral and cognitive homology as well (e.g. Allen and Fortin 2013). Ginsburg and Jablonka (2019: 329, 339) conjecture that associative learning can take on different forms and be subject to different limitations on what can be learned and how depending on different brain architectures in different taxa. Feest (2025) considers how neurological kinds might play constitutive roles in creating cognitive character hierarchies. It may be that bilaterian animal nervous systems are necessary for particular forms of behavioral and cognitive flexibility, and subtypes of these nervous systems are necessary for specific variants of these forms.

4. Remarks on Consciousness

I have adopted a biology-first (not biology-only) perspective on the new mind/body problem, given that the bulk of the empirical results motivating it involve biological organisms. In this section I will consider how the reformulation impacts our thinking about consciousness. For many, the mind/body problem *just is* the problem of how consciousness is related to body, so it cannot be ignored. However, for space reasons, my discussion is schematic and can only anticipate more extensive treatment.

The consciousness/body problem is discussed in two largely separate conversations, depending on whether "body" is interpreted as "biological body" or "anything physical". This may be due in part to Chalmers' (1995a) division of consciousness problems into the easy problems and the hard problem, and in part to a longstanding lack of (even aversion to) research into nonhuman consciousness. Regardless, there is clearly the basic difficulty of operationalizing consciousness in the absence of verbal report, a problem that also affects very young and impaired humans as well as any nonhuman entity.

Within the "biological body" camp, the distribution question prompts the search for reliable indicators of "what it's like" (Nagel 1974) in the absence of verbal report. Often these indicators are brain-based, such as requiring prefrontal cortex, a brain stem, or a brain evolved

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

enough to support more complex forms of associative learning (Barron and Klein 2016; Birch et al. 2020; Ginsburg and Jablonka 2019). Birch (2020) offers a behavior-based proposal in which we can reliably infer to consciousness to different species and taxa if they exhibit at least some of a cluster of cognitive abilities, such as trace conditioning, that are facilitated by consciousness when humans exhibit them. These approaches bring what we know about the phylogenetic distribution of brains and cognition directly to bear on claims about the phylogenetic distribution of consciousness.

The diversity question is being addressed in attempts to characterize consciousness in ways that go beyond an undifferentiated "what it's like" property and unstable or idiosyncratic ways of distinguishing the referents of "qualia", "sentience", "subjective experience", and "phenomenal consciousness". As indicated above, the key metaphysical issue is to distinguish the features of human conscious states that are unique to our phenotype and the features that may be shared with nonhuman conscious states. For example, Godfrey-Smith (2016, 2020) defends a gradualist theory of consciousness, with earlier- and later-evolving types, as well as a distinction between subjective experiential states (such as pain) from broader states of consciousness, and an analysis of human conscious experience into sensory and evaluative dimensions that need not be co-instantiated. A helpful analogy (or guide) for this emerging diversity of types may be the way biologists distinguish vision-related abilities and their associated structures (Nilsson 2013). These range from photosensitivity to high-resolution vision, where the former is widespread and the latter less so – although high-resolution eyes evolved convergently dozens of times in different lineages due to its adaptive benefits. Similarly, there may be subjective experiential states analogous to undirected and directed photosensitivity, simple forms of consciousness analogous to low-resolution vision, and "what it's like" consciousness analogous to high-resolution vision. If we end up agreeing that birds, amphibians, cephalopods, and bees are "what it's like" conscious, the analogy may be even more apt, with convergent evolution of "what it's like" across major clades and more fine-grained consciousness characters within clades.

Meanwhile, within the "any physical body" camp, debate about consciousness is anchored in computational modeling and a subset of neuroscience facts, mostly from human brains. The main concern here is whether artificial neurons or non-existent but allegedly physically possible beings with neurons in nonstandard configurations could be conscious (Chalmers 1995b; Schwitzgebel 2015). The affirmative side relies on the principle of medium (or

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

substance) independence in standard functionalism, according to which mental states are defined by their functional roles and not by the material stuff that realizes the roles.[3]

As a result of this bifurcation, the question of whether a brain is necessary for consciousness is ambiguous. If we are considering consciousness in biological bodies, the question is interpreted as: Is a brain, as opposed to simpler neuronal or nonneuronal mechanisms, necessary for consciousness? If a brain is necessary, then cnidaria and ctenaphora (as well as placozoa and porifera) cannot be conscious among animals, while cephalopod molluscs and decapod crustaceans may be. Notably, asking the biological question is not an example of chauvinism (Block 1980). There are biological counterfactuals whose truth conditions are such that (for example) it is either true or false that if an organism does not have a brain it does not have consciousness. As Birch et al (2022: 5) expressly state, they offer sufficiency criteria for consciousness in living organisms given the actual laws of nature. They are not engaging in a debate with Chalmers.

On the other hand, if we are considering consciousness in any physical body, then the question is interpreted as: is a brain, as opposed to artificial structures or any non-living material, necessary? For example, Chirimuuta (2018) and Cao (2022) argue, *pace* Chalmers, that neuroscientific details of various kinds make it highly unlikely that consciousness can be realized by artificial neurons. Given this interpretation of "body" and the associated reliance on metaphysical rather than biological necessity, Chalmers or Schwitzgebel are unlikely to be bothered; they can update their hypothetical scenarios to encompass the allegedly relevant details, and those who think this isn't sufficient may be accused (justly or not) of chauvinism. In addition, the research on associative learning in simple animals shows we don't know yet what exactly about brains, or even neurons with synapses, is relevant or necessary for at least some aspects of mind. The issue of relevant neural details in the artificial consciousness debate lacks needed input from the biologists.

Other than encouraging more cross-talk between participants in these debates, I see two (consistent) ways to move forward given the duality of consciousness/body problems. One is to acknowledge a deeper ambiguity. By asking the diversity question, we are thinking beyond the

[3] An intermediate case between the "biological" and "any physical" body camps is Segundo-Ortin and Calvo 2022, who use morphological and functional analogies between plants and animals to try to shift the burden of proof to those who deny plant consciousness.

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

use of human consciousness phenotypes to define consciousness. So we can ask whether the sort of consciousness in a biological organism is the same as that which is being ascribed to artificial or hypothetical agents. If Chalmers or Schwitzgebel are positing a distinct kind of computer or weird-body consciousness, everyone could be right, albeit about different things. We would just need to disambiguate what type of consciousness we're talking about – the evolved biological sort, and the sort we might ascribe to computers or weird bodies. Alternatively, proponents of computer or weird-body consciousness need to defend their assumption that these entities realize the same type of consciousness as the biological ones. Even if we agree computers could be conscious, conceivability is insufficient evidence for asserting that what they have is the same as what biological organisms have.

The second way forward is to understand the nature of biological modality a lot better than we do. The biology-first perspective adopted here is based in the conviction that the truth values of modal claims about nonbiological minds should be constrained by our understanding of biological necessity and other biological modal claims. The latter provides a firm empirical basis for decisions regarding which differences between biological and artificial systems are relevant for ascribing any mental phenomenon to an artificial system. Without these constraints, our theorizing about nonbiological consciousness will remain mired in what Birch (2024: 47) aptly calls "a game of evidence-free speculation".

5. Concluding Summary.

I've argued that the 21st century form of the mind-body problem should (and is being) reconceived to acknowledge the need to explain the diversity and distribution of mind, including consciousness, as well as the diversity and distribution of body. This transformation of the problem involves more than just taking more species, more clades, and more biological mechanisms into consideration. It requires a new conceptual and metaphysical repertoire that includes characters and relations between them, especially homology, and the development of a nested hierarchy of mind characters individuated at multiple grain sizes. Epistemologically, claims of reduction or non-reduction are subject to new restrictions in their scope to match the phylogenetic distribution of the mind character that may be reduced and the different types of evidence required depending on whether the character is shared across species by homology or homoplasy. It requires articulating the non-contingent relationships that may hold between mind

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

and body character definitions and mind/body mappings. Finally, it reveals ambiguity in current debates about the consciousness/body problem and the relation of biological and artificial (or hypothetical) types of consciousness.

Acknowledgements: Many thanks to Adrian Currie, Anton Killin, Noam Miller, Gunter Wagner, and Lauren Wilson for their insights and participation in the PSA 2024 Symposium "Cognition and Phylogeny: Integrating Tree-Thinking into Psychology", and to our audience for questions and feedback. I also thank audiences and organizers of the Sino-Australian Philosophy of Life Sciences Network 2024 conference on Evolution and Development at the Institute for Philosophy of the Chinese Academy of Sciences, the University of Pittsburgh Center for Philosophy of Science for a Featured Former Fellow talk in January 2025, and the Active Mind group at the University of Edinburgh for additional feedback at various stages of development of the ideas in this paper. Finally, I would like to thank the Stanley-University of Iowa Foundation Support Organization for their generous travel support for my attendance at PSA 2024.

Funding Statement. None to declare.

Declarations. None to declare.

References

Abramson, C. I., & Wells, H. (2018). An inconvenient truth: Some neglected issues in invertebrate learning. Perspectives on Behavior Science, 41(2), 395-416. https://doi.org/10.1007/s40614-018-00178-8

Adelman, B. E. (2018). On the conditioning of plants: A review of experimental evidence. Perspectives on Behavior Science, 41(2), 431-446. https://doi.org/10.1007/s40614-018-0173-6

Alberch, P., & Gale, E. A. (1985). A developmental analysis of an evolutionary trend: digital reduction in amphibians. Evolution, 39(1), 8-23. https://doi.org/10.1111/j.1558-5646.1985.tb04076.x

Allen, C. (2017). On (not) defining cognition. Synthese, 194(11), 4233-4249. https://doi.org/10.1007/s11229-017-1454-4

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

Allen, J. A. (2019). Community through culture: From insects to whales: How social learning and culture manifest across diverse animal communities. BioEssays, 41(11), 1900060. https://doi.org/10.1002/bies.201900060Digital Object Identifier (DOI)

Allen, T. A., & Fortin, N. J. (2013). The evolution of episodic memory. Proceedings of the National Academy of Sciences, 110(supplement_2), 10379-10386. https://doi.org/10.1073/pnas.1301199110

Barron, A.B., Hebets, E.A., Cleland, T.A., Fitzpatrick, C.L., Hauber, M.E. and Stevens, J.R., 2015. Embracing multiple definitions of learning. Trends in neurosciences, 38(7), pp. 405-407. https://doi.org/10.1016/j.tins.2015.04.008

Barron, A. B., & Klein, C. (2016). What insects can tell us about the origins of consciousness. Proceedings of the National Academy of Sciences, 113(18), 4900-4908. https://doi.org/10.1073/pnas.1520084113

Bielecki, J., Nielsen, S.K.D., Nachman, G. and Garm, A., 2023. Associative learning in the box jellyfish Tripedalia cystophora. Current Biology, 33(19), pp.4150-4159. https://doi.org/10.1016/j.cub.2023.08.056

Birch, J. (2022). The search for invertebrate consciousness. Noûs, 56(1), 133-153. https://doi.org/10.1111/nous.12351

Birch, J., Schnell, A. K., & Clayton, N. S. (2020). Dimensions of animal consciousness. Trends in cognitive sciences, 24(10), 789-801. https://doi.org/10.1016/j.tics.2020.07.007

Birch, J. (2024). The edge of sentience: risk and precaution in humans, other animals, and AI (p. 398). Oxford University Press. https://doi.org/10.1093/9780191966729.001.0001

Block, N. (1978). Troubles with Functionalism. In C. Savage ed., Perception and Cognition: Issues for the Foundations of Psychology. Minneapolis: University of Minneapolis Press, 261-325. https://doi.org/10.7551/mitpress/2111.003.0006

Broad, C. D. (1925/ 2014). The mind and its place in nature. Routledge. https://doi.org/10.4324/9781315824147

Burkhardt, R. W. (2005). Patterns of behavior: Konrad Lorenz, Niko Tinbergen, and the founding of ethology. University of Chicago Press. https://doi.org/**10.1002/jhbs.20151**

Cao, R. (2022). Multiple realizability and the spirit of functionalism. Synthese, 200(6), 506. https://doi.org/10.1007/s11229-022-03524-1

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

Chalmers, D. J. (1995a). Facing up to the problem of consciousness. Journal of consciousness studies, 2(3), 200-219. https://doi.org/10.1007/s11229-022-03524-1

Chalmers, D. J. (1995b). Absent qualia, fading qualia, dancing qualia. In T. Metzinger, ed., Conscious experience (Ferdinand Schoningh): 309-328.

Chen, Z., & Wiens, J. J. (2020). The origins of acoustic communication in vertebrates. Nature communications, 11(1), 369. https://doi.org/10.1038/s41467-020-14356-3

Cheng, K. (2023). Learning in Cnidaria: a summary. Communicative & Integrative Biology, 16(1), 2240669. https:// DOI: 10.1080/19420889.2023.2240669

Chirimuuta, M. (2018). Marr, Mayr, and MR: What functionalism should now be about. Philosophical Psychology, 31(3), 403-418. https://doi.org/10.1080/09515089.2017.1381679

Cisek, P. (2019). Resynthesizing behavior through phylogenetic refinement. Attention, perception, & psychophysics, 81, 2265-2287. https://doi.org/ 10.3758/s13414-019-01760-1

Coombs, S., & Trestman, M. (2025). A multi-trait embodied framework for the evolution of brains and cognition across animal phyla. Behavioral and Brain Sciences 48, e77. https://doi.org/10.1017/S0140525X24000335

Darwin, C. (1859/1993). The origin of species. New York: Random House.

De Waal, F. B., & Ferrari, P. F. (2010). Towards a bottom-up perspective on animal and human cognition. Trends in cognitive sciences, 14(5), 201-207. https://doi.org/ 10.1016/j.tics.2010.03.003

Ereshefsky, M. (2012). Homology thinking. Biology & Philosophy, 27, 381-400. https://doi.org/10.1007/s10539-012-9313-7

Feest, U. (2025). Operationism in psychology: An epistemology of exploration. In Operationism in Psychology. University of Chicago Press.

Figdor, C. (2024). Individuating cognitive characters: Lessons from praying mantises and plants. Philosophy of science, 91(4), 930-949. https://doi.org/10.1017/psa.2024.10

Gagliano, M., Vyazovskiy, V. V., Borbély, A. A., Grimonprez, M., & Depczynski, M. (2016). Learning by association in plants. Scientific reports, 6(1), 38427. https://doi.org/: 10.1038/srep38427

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

Ginsburg, S., & Jablonka, E. (2010). The evolution of associative learning: A factor in the Cambrian explosion. Journal of theoretical biology, 266(1), 11-20. https://doi.org/10.1016/j.jtbi.2010.06.017

Ginsburg, S., & Jablonka, E. (2019). The evolution of the sensitive soul: Learning and the origins of consciousness. MIT Press. https://doi.org/10.7551/mitpress/11006.001.0001

Godfrey-Smith, P. (2016). Mind, matter, and metabolism. The Journal of Philosophy, 113(10), 481-506. https://doi.org/10.5840/jphil20161131034

Godfrey-Smith, P. (2020). Varieties of subjectivity. Philosophy of Science, 87(5), 1150-1159. https://doi.org/10.1086/710541

Griffiths, P. (1997). What Emotions Really Are: The problem of psychological categories. University of Chicago Press, Chicago. https://doi.org/10.7208/chicago/9780226308760.001.0001

Herculano-Houzel, S. (2012). The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost. Proceedings of the National Academy of Sciences, 109(supplement_1), 10661-10668. https://doi.org/ 10.1073/pnas.1201895109

Heyes, C. (2018). Cognitive gadgets: The cultural evolution of thinking. Harvard University Press. https://doi.org/10.4159/9780674985155

Jarvis, E. D. (2019). Evolution of vocal learning and spoken language. Science, 366(6461), 50-54. https://doi.org/ 10.1126/science.aax0287

Jarvis, E.D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D.J., Shimizu, T. and Striedter, G., 2005. Avian brains and a new understanding of vertebrate brain evolution. Nature Reviews Neuroscience, 6(2), pp.151-159. https://doi.org/ 10.1038/nrn1606

Jékely, G., Keijzer, F., & Godfrey-Smith, P. (2015). An option space for early neural evolution. Philosophical Transactions of the Royal Society B: Biological Sciences, 370(1684), 20150181. https://doi.org/ 10.1098/rstb.2015.0181

Khalidi, M. A. (2023). Cognitive Ontology. Cambridge University Press. https://doi.org/10.1017/9781009223645

Kim, J. (1972). Phenomenal properties, psychophysical laws, and the identity theory. The Monist, 177-192. https://doi.org/10.5840/monist19725623

Loy, I., Carnero-Sierra, S., Acebes, F., Muñiz-Moreno, J., Muñiz-Diez, C. and Sánchez-González, J.C., 2021. Where association ends. A review of associative learning in invertebrates,

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

plants and protista, and a reflection on its limits. Journal of Experimental Psychology: Animal Learning and Cognition, 47(3), p.234. https://doi.org/10.1037/xan0000306

Lyon, P., Keijzer, F., Arendt, D., & Levin, M. (2021). Reframing cognition: getting down to biological basics. Philosophical Transactions of the Royal Society B, 376(1820), 20190750. https://doi.org/ 10.1098/rstb.2019.0750

MacLean, E.L., Matthews, L.J., Hare, B.A., Nunn, C.L., Anderson, R.C., Aureli, F., Brannon, E.M., Call, J., Drea, C.M., Emery, N.J. and Haun, D.B., 2012. How does cognition evolve? Phylogenetic comparative psychology. Animal cognition, 15, pp.223-238. https://doi.org/ 10.1007/s10071-011-0448-8

Maturana, H. R., & Varela, F. J. (1991). Autopoiesis and cognition: The realization of the living (Vol. 42). Springer Science & Business Media.

Meyerowitz, E. M. (2002). Plants compared to animals: the broadest comparative study of development. Science, 295(5559), 1482-1485. https://doi.org/ 10.1126/science.1066609

Moroz, L. L., & Romanova, D. Y. (2022). Alternative neural systems: What is a neuron? (Ctenophores, sponges and placozoans). Frontiers in Cell and Developmental Biology, 10, 1071961. https://doi.org/10.3389/fcell.2022.1071961

Moroz, L. L., & Romanova, D. Y. (2021). Selective advantages of synapses in evolution. Frontiers in Cell and Developmental Biology, 9, 726563. https://doi.org/10.3389/fcell.2021.726563

Nagel, T. (1974). What is it like to be a bat? Philosophical Review 83 (4): 435-450. https://doi.org/10.2307/2183914

Nilsson, D. E. (2013). Eye evolution and its functional basis. Visual neuroscience, 30(1-2), 5-20. https://doi.org/ 10.1017/S0952523813000035

Owen, R. (1848). On the archetype and homologies of the vertebrate skeleton. John van Voorst, London.

Papini, M. R. (2002). Pattern and process in the evolution of learning. Psychological review, 109(1), 186. https://doi.org/ 10.1037/0033-295x.109.1.186

Papini, M. R. (2024). Behavioral plasticity in aneural organisms. Psychological Review 132 (5): 1074-1089. https://doi.org/10.1037/rev0000483

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press

Poldrack, R. A., & Yarkoni, T. (2016). From brain maps to cognitive ontologies: informatics and the search for mental structure. Annual review of psychology, 67(1), 587-612.https://doi.org/ 10.1146/annurev-psych-122414-033729

Pontes, A. C., Mobley, R. B., Ofria, C., Adami, C., & Dyer, F. C. (2020). The evolutionary origin of associative learning. The american naturalist, 195(1), E1-E19. https://doi.org/10.1086/706252

Prados, J. (2023). Disentangling the evolution of cognition: Learning in Cnidaria. Learning & Behavior, 1-2. https://doi.org/ 10.3758/s13420-023-00621-0

Ramsey, G. (2013). Culture in humans and other animals. Biology & Philosophy, 28, 457-479. https://doi.org/10.1007/s10539-012-9347-x

Schwitzgebel, E. (2015). If materialism is true, the United States is probably conscious. Philosophical Studies, 172, 1697-1721. https://doi.org*10.1007/s11098-014-0387-8*

Segundo-Ortin, M., & Calvo, P. (2022). Consciousness and cognition in plants. Wiley Interdisciplinary Reviews: Cognitive Science, 13(2), e1578. https://doi.org/*10.1002/wcs.1578*

Taylor, A. H., Bastos, A. P., Brown, R. L., & Allen, C. (2022). The signature-testing approach to mapping biological and artificial intelligences. Trends in Cognitive Sciences, 26(9), 738-750. *https://doi.org/10.1016/j.tics.2022.06.002*

Van Duijn, M. (2017). Phylogenetic origins of biological cognition: convergent patterns in the early evolution of learning. Interface Focus, 7(3), 20160158. *http://dx.doi.org/10.1098/rsfs.2016.0158i*

Wagner, G. P. (Ed.). (2000). The character concept in evolutionary biology. Elsevier. https://doi.org/10.1016/B978-0-12-730055-9.X5005-8

Westra, E., Fitzpatrick, S., Brosnan, S.F., Gruber, T., Hobaiter, C., Hopper, L.M., Kelly, D., Krupenye, C., Luncz, L.V., Theriault, J. and Andrews, K., 2024. In search of animal normativity: a framework for studying social norms in non-human animals. Biological Reviews, 99(3), pp.1058-1074. https://doi.org/ *10.1111/brv.13056*

Whiten, A., Horner, V., & De Waal, F. B. (2005). Conformity to cultural norms of tool use in chimpanzees. Nature, 437(7059), 737-740. https://doi.org*10.1038/nature04047*

https://doi.org/10.1017/psa.2026.10274 Published online by Cambridge University Press