



RESEARCH ARTICLE

# Children of time: the geological recency of intelligence and its implications for SETI

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## Abstract

Of all species on Earth, only one – *Homo sapiens* – has developed a technological civilization. As a consequence, estimates of the number of similar civilizations beyond Earth often treat the emergence of human-like intelligence or ‘sophonce’ as an evolutionary unicum: a contingent event unlikely to repeat itself even in biospheres harbouring complex brains, tool use, socially transmitted behaviours and high general intelligence. Here, attention is drawn to the unexpected recency and temporal clustering of these evolutionary preconditions to sophonce, which are shown to be confined to the last  $\leq 10^2$  million years. I argue that this pattern can be explained by the exponential biotic diversification dynamics suggested by the fossil record, which translated into a nonlinearly expanding range of cognitive and behavioural outcomes over the course of Earth’s history. As a result, the probability of sophonce arising out of a buildup of its enabling preconditions has been escalating throughout the Phanerozoic. The implications for the Silurian hypothesis and the search for extraterrestrial intelligence (SETI) are discussed. I conclude that the transition from animal-grade multicellularity to sophonce is likely not a rate-limiting step in the evolution of extraterrestrial technological intelligences, and that while *H. sapiens* is probably the first sophont to evolve on Earth, on macroevolutionary grounds it is unlikely to be the last.

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## Introduction

The Drake equation (Drake, 1961, 1965) offers a useful roadmap to lay out limiting factors to the frequency of observable extraterrestrial intelligences. In Drake's probabilistic argument, the number of technological civilizations detectable by radioastronomy ( $N$ ) is a product of the following: the average rate of star formation in the galaxy ( $R^*$ ), the fraction of stars with a planetary system ( $f_p$ ), the average number of habitable planets per star ( $n_e$ ), the fraction of these on which life eventually arises ( $f_l$ ), the fraction of such biospheres in which intelligent lifeforms able to develop a technological civilization (henceforth 'sophonts', after Wright *et al.*, 2018) will evolve ( $f_i$ ), the fraction of sophonts that develop to emit detectable forms of communication ( $f_c$ ) and the temporal duration ( $L$ ) of such communications.

Each variable in Drake's equation can be decomposed virtually *ad infinitum* into a series of further terms. Factored into  $f_l$  are the probabilities of classical 'major evolutionary transitions' (Szathmáry and Smith, 1995), including eukaryogenesis and complex multicellularity or exobiological analogues thereof (Levin *et al.*, 2019). As shown by the millions of non-sophont multicellular eukaryotes on Earth (Mora *et al.*, 2011; Larsen *et al.*, 2017), these major evolutionary steps are necessary but insufficient preconditions for technological civilization to arise (Levin *et al.*, 2019). For *Homo sapiens* to evolve into a civilization-building species, additional 'minor' or proximate transitions were required. Among them was the transition from an animal-grade organization, combining complex multicellularity and heterotrophic habits (Butterfield, 2011; Knoll, 2011; Cavalier-Smith, 2017), to sophonce *sensu* Wright *et al.* (2018). This proximate transition can be factored into Drake's equation as  $f_s$ : the fraction of biospheres where animal-grade organisms give rise to  $N \geq 1$  sophont species.  $f_s$  will be the focus of the present paper.

Whereas the astrophysical terms of Drake's equation ( $R^*$ ,  $f_p$  and  $n_e$ ) have all been constrained observationally (Frank and Sullivan, 2016), the history and properties of life on Earth provide the only available starting points to estimate the value of the 'biotic' terms, including  $f_s$ . In this respect, a sample size of 1 biosphere is suboptimal, but far from uninformative (Simpson, 2015). The timing and frequency of abiogenesis, major evolutionary transitions and other evolutionary events in Earth's history have all been analysed to extrapolate their cosmic probabilities and identify rate-limiting 'critical steps' in extraterrestrial technological intelligence (ETI) evolution (Watson, 2008; Spiegel and Turner, 2012; Kipping, 2020; Snyder-Beattie *et al.*, 2021).

Evolutionary analyses of intelligence's likelihood must inevitably factor in observer selection effects – the correlations between the observation of given properties and the existence of the observer in the first place (Bostrom, 2013). Given selection effects, any observer assessing the frequency of intelligence in the universe must necessarily spawn from a biosphere where all preconditions to sophonce were met at least once – that is, in the observer's own lineage. However, for the observer to exist, these preconditions need not have been met multiple times independently, hampering the assessment of their likelihood. In this light, the study of evolutionary histories beyond the observer's own lineage (e.g. Conway Morris, 2003; Martinez, 2014; Roth, 2015) offers a precious independent source of evidence to infer which preconditions to ETI are most and least likely to obtain (Powell, 2020).

Human sophonce rests on the unique 'ratchet' of open-ended cumulative cultural evolution (CCE), by which stepwise improvements in cultural products are retained and elaborated upon across generations (Tennie *et al.*, 2009; Powell, 2020). This trait distinguishes humans from other species known to produce socially transmitted technologies (Tennie *et al.*, 2009), none of which qualifies as sophont *sensu* Wright *et al.* (2018). Its uniqueness is often taken to imply a conspiracy of evolutionary contingencies unlikely to be repeated in Earth's future or in extraterrestrial biospheres – 'even those that evolve complex brains, sociality, and intelligence broadly conceived' (Powell, 2020). This scenario corresponds to extremely low values for  $f_s$  and, all else being equal,  $N$ : to produce technological signatures observable over interstellar distances (e.g. Drake, 1961, 1965; Ćirković, 2006; Bradbury *et al.*, 2011; Beatty, 2022; Haqq-Misra *et al.*, 2022a, 2022b) CCE stands out as a minimal prerequisite (Powell, 2020).

Importantly, however, human CCE stands on a cumulated set of necessary evolutionary preconditions or 'exaptations' (Gould and Vrba, 1982). Minimally, these include high domain-general

intelligence (Chiappe and MacDonald, 2005), sociality (Ward and Webster, 2016), tool use (Van Lawick-Goodall, 1971) and culture, defined as socially transmitted group-level behaviour (Laland and Galef, 2009), together with any putative cognitive or behavioural unicum of *H. sapiens*. While CCE itself has appeared only once on Earth, at least some of its enabling exaptations have evolved repeatedly, and often in combination, in different lineages (e.g. Ćirković, 2018a).

Here, the likelihood of an extremely low  $f_s$  value is assessed by considering not only the phylogenetic spread of CCE exaptations but also their timing of origin relative to the evolutionary events bracketing  $f_s$  – the appearance of animal-grade organisms and that of human sophonce itself. First, palaeontological proxies and phylogenetic comparisons will be used to map the timing of the evolution of CCE preconditions in intelligent, social, tool-using animals, including primates, cetaceans, proboscideans, corvids, parrots and cephalopods. Next, the plausibility of the ‘Silurian hypothesis’ – the proposal that humans are not the first civilization-building species to evolve on Earth (Schmidt and Frank, 2019) – will be assessed through the lens of the fossil record, strengthening the case for the geological recency of CCE preconditions. The merits of ‘long-fuse’ (Bogonovich, 2011) and step-based models of cognitive evolution will then be discussed in light of this phenomenon. Based on intelligence’s timing and phylogenetic spread and the tempo of cognitive evolution in *H. sapiens*’ own lineage, the following hypotheses will be laid out:

1. On Phanerozoic Earth, the first-order control on the evolution of intelligence has been the supply rate of evolutionary novelty and not the availability of permissive global geobiological conditions.
2. The transition from animal-grade multicellularity to sophonce is not a rate-limiting factor to  $N$ .
3. Contrary to the ‘Silurian hypothesis’ (Schmidt and Frank, 2019), *H. sapiens* is most likely the first sophont to evolve on Earth.
4. All else being equal, in biospheres harbouring animal-grade multicellularity the temporal frequency and permanence of sophonce can be expected to increase nonlinearly as a function of time.

### The evolutionary recency of CCE exaptations

CCE preconditions including flexible tool use (Boire *et al.*, 2002; Overington *et al.*, 2009; Shumaker *et al.*, 2011; Heldstab *et al.*, 2016), sociality (Dunbar, 2009; Shultz, and Dunbar, 2010), innovativeness (Sol *et al.*, 2022) and general problem-solving and learning abilities (Jerison, 1985; Reader and Laland, 2002; Rushton, and Ankney, 2009; Benson-Amram *et al.*, 2016) all positively correlate with measures of relative brain size across phylogenetically disparate taxa, suggesting that these indicators represent imperfect but informative proxies for ‘intelligence’ (Smaers *et al.*, 2021). In particular, the encephalization quotient (EQ), the ratio between observed and predicted brain mass for a given body size (Jerison, 1973), provides a useful comparative measure that is widely applicable across vertebrates. EQ can be defined mathematically as  $EQ = E_a/E_e$ , where  $E_a$  is the actual brain mass for a given taxon and  $E_e$  is its expected value based on nonlinear regression on brain mass scores across the taxonomic group of reference (e.g. mammals; Jerison, 1973). EQ can be adjusted to account for the effects of phylogenetic non-independence, yielding a ‘phylogenetic EQ’ score (PEQ; Ni *et al.*, 2019).

By combining EQ proxies with complementary data from the neuroanatomy of living and fossil species (e.g. Knoll and Kawabe, 2020) and comparative cognition, the non-uniformity of animal intelligence through geological time has been established at multiple taxonomic scales. Long-term macroevolutionary increases in mean and maximum encephalization, neural complexity and the size of brain areas devoted to higher cognition have been convincingly documented in birds (e.g. Ksepka *et al.*, 2020; Stacho *et al.*, 2020), mammals (e.g. Jerison, 1973, 1994; Smaers *et al.*, 2018, 2021; Bertrand *et al.*, 2022) and vertebrates as a whole (e.g. Russell, 1983; Northcutt, 2002; Rospars, 2010). Likewise, both phylogenetic bracketing and palaeontological proxies for cognitive abilities indicate that the appearance of CCE exaptations in vertebrates is a geologically recent phenomenon, largely postdating the Eocene epoch (56–33.9 million years ago – Mya). This pattern holds true for those lineages conventionally thought to comprise the most ‘intelligent’, socially complex and technologically capable nonhumans, including primates, cetaceans, proboscideans, corvids and parrots.

### *Primates*

Endocasts of stem-group primates, which first appear in the fossil record in the Palaeocene (~66 Mya; Wilson Mantilla *et al.*, 2021), show limited neocortical development and relative brain sizes almost universally lower than those of any living prosimians (i.e. strepsirrhines and tarsiers), with some falling below the mammalian EQ average. Together, these proxies (Gingerich and Gunnell, 2005; Silcox *et al.*, 2009; Harrington *et al.*, 2016) suggest a lack of complex sociality and high domain-general intelligence. Even among crown-group primates, the convergent evolution of CCE exaptations (e.g. Ottoni and Izar, 2008) is circumscribed to anthropoids – the clade comprising platyrrhines ('New World' monkeys) and catarrhines ('Old World' monkeys, including humans).

Both Old and New World monkeys comprise multiple lineages of highly social, cognitively sophisticated tool users. A vast literature attests to the social intelligence (e.g. de Waal, 1982; Tomasello and Call, 1994; Tomasello, 2022), flexible problem-solving (e.g. Emery and Clayton, 2004; Schmitt *et al.*, 2012), culture (e.g. Whiten *et al.*, 1999; Van Schaik *et al.*, 2003; Schofield *et al.*, 2018) and technological capabilities (e.g. Boesch and Boesch, 1990; Van Schaik *et al.*, 1996; Malaivijitnond *et al.*, 2007; Carvalho *et al.*, 2009) of catarrhines, including apes. In recent decades, the same traits have increasingly been documented in platyrrhines, with particular attention devoted to the problem-solving skills (Fragaszy and Cummins-Sebree, 2005) and tool-use traditions of capuchin monkeys (Ottoni and Izar, 2008).

Since their >36 million years (Myr) old Eocene split (Bond *et al.*, 2015), platyrrhines and catarrhines attained high encephalization levels independently, as revealed by comparisons among living and fossil anthropoids. Ancestral states reconstructions based on fossil endocasts of stem-group platyrrhines and catarrhines suggest that a PEQ of about 1 – comparable to those of the non-tool-using, solitary prosimian tarsiers – represents the ancestral condition for both lineages (Ni *et al.*, 2019); in contrast, PEQs > 3 occur in both living platyrrhines and catarrhines, with most apes falling in the 3–4 range (Ni *et al.*, 2019).

Less emphasized in the astrobiological literature is the fact that encephalization and cerebral complexification are also recurring themes *within* both the catarrhine and platyrrhine clades (Reader *et al.*, 2011). Phylogenetically informed comparisons of fossil endocasts suggest that encephalization, an accompanying shrinkage of olfactory bulbs and the emergence of the convoluted neocortex associated with higher cognitive abilities such as tool use and sociality occurred independently in the two catarrhine subgroups – cercopithecoids and hominoids (Gonzales *et al.*, 2015) – within the last 17–18 Myr. Overall, the evidence from comparative cognition and neuroanatomy indicates that high general intelligence almost certainly evolved convergently at least three times in catarrhines from the Miocene onwards: in baboons, macaques and apes (Reader *et al.*, 2011). Likewise, PEQs in the 3–4 range evolved independently in the social, highly encephalized spider monkeys and tool-using capuchins (Wildman *et al.*, 2009; Ni *et al.*, 2019) after the origins of the platyrrhine crown-group around 20.8–27.0 Mya (Beck *et al.*, 2023). This strongly suggests that anthropoids combined high general intelligence, culturally transmitted technologies and complex sociality no earlier than the latest Oligocene.

### *Cetaceans*

Cetaceans have been found to match or outperform anthropoids in mnemonic and metacognitive problem-solving and assemble some of the most complex societies of all nonhuman animals (Marino, 2017; Connor *et al.*, 2022). Social learning in cetaceans has precipitated the emergence of cultures at multiple scales of social organization, with some centred on tool use (Noad *et al.*, 2000; Rendell and Whitehead, 2003; Whitehead and Rendell, 2004; Helweg *et al.*, 2005; Krützen *et al.*, 2005; Garland *et al.*, 2011, 2022; Allen *et al.*, 2013; Wild *et al.*, 2020; Ramos *et al.*, 2021). In some species, such as orcas (*Orcinus orca*), cultural niches may be sufficiently entrenched to drive the kind of gene-culture 'coevolution' traditionally seen as a hallmark of hominin history (Foote

*et al.*, 2016). However, beyond their basic eutherian groundplan the cytoarchitectures of cetacean and primate brains are fundamentally distinct, clearly reflecting a long Cenozoic history of independent evolution (Marino, 2002, 2017).

The earliest cetaceans evolved from archaic ungulates akin to the Eocene (~48 Myr old) *Indohyus*. This animal had a plesiomorphic mammalian brain with a small and simply folded neocortex (Orliac and Thewissen, 2021). Accordingly, the EQ of the LCA of cetaceans and their living sister-group – hippos – has been estimated at 0.465, well below the mammalian average (Montgomery *et al.*, 2013). Endocasts of the first fully aquatic cetaceans, the Palaeogene (~53 to ~30 Myr ago) Archaeoceti, show very limited change in EQ relative to this ancestral baseline (Montgomery *et al.*, 2013; Marx *et al.*, 2016; Marino, 2022).

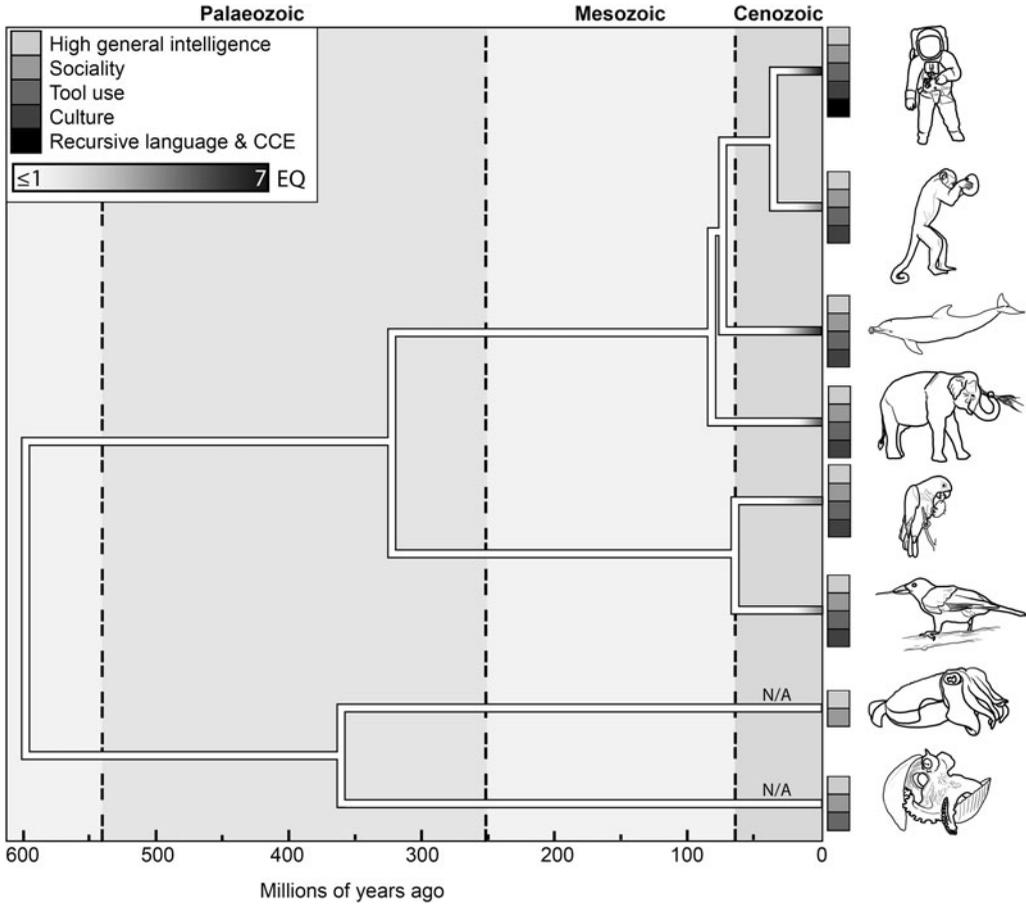
In contrast, the mid-late Cenozoic witnessed two major encephalization pulses in cetaceans, accompanied by significant cortical expansion and restructuring (Marino *et al.*, 2004; Montgomery *et al.*, 2013; Marino, 2022). The first occurred with the Oligocene (~35 Myr ago) emergence of the Neoceti, comprising present-day baleen (Mysticeti) and toothed whales (Odontoceti). The Oligocene saw a marked upward shift in encephalization relative to the archaeocete baseline: the estimated EQ of the neocete LCA (~1.383) is well within the modern toothed whale range (Montgomery *et al.*, 2013). Odontocetes experienced a further encephalization pulse at the base of the delphinoid clade, which originated around 15–20 Mya (Fig. 1). Delphinoids comprise the most cognitively sophisticated cetaceans, with neocortex folding and encephalization levels in dolphins (EQs ~4–5) surpassing those of all nonhuman primates (Marino *et al.*, 2004; Montgomery *et al.*, 2013; Marino, 2017; Smaers *et al.*, 2021). In some delphinoid lineages, the pace of encephalization within the last 10 Myr outstripped that of hominins (Montgomery *et al.*, 2013), showing that human brain enlargement is not unique in its recent accelerando (Püschel *et al.*, 2021).

### **Proboscideans**

Proboscideans offer further evidence for mammalian intelligence being phylogenetically disparate, ecologically unconstrained and geologically recent. While elephant toolmaking in the wild is restricted to ‘fly swats’ manufactured by breaking off branches (Hart *et al.*, 2001; Bates *et al.*, 2008), captive elephants can exploit a range of unfamiliar tools using their remarkably versatile manipulatory trunk (Shoshani, 1997) and possibly solve physical cognition tasks by insight (Foerder *et al.*, 2011). Further, elephants display exceptionally strong mnemonic (McComb *et al.*, 2001, 2014; Byrne *et al.*, 2009) and numerical skills among nonhuman animals (Irie *et al.*, 2019) and manifest social learning within complex fission-fusion societies (Lee and Moss, 1999; Byrne *et al.*, 2008, 2009). These capacities rest on large brains with significant cytoarchitectural differences from those of primates or cetaceans, from which they split as far back as the late Cretaceous (Hart *et al.*, 2008) and that share with elephants the basic cellular architecture and macrostructure common to all placental mammals (Bertrand *et al.*, 2022).

The earliest fossil proboscideans, exemplified by the Eocene (~35 Myr ago) *Moeritherium*, had an EQ of about 0.2 – a value approaching that of sirenians, the proboscidean sister-group (O’Shea and Reep, 1990; Upham *et al.*, 2019). From this baseline well below the modern mammalian average, brain enlargement in proboscideans was matched by increases in body mass until the Oligocene, around 30 Myr, when sustained stepwise encephalization began (Benoit *et al.*, 2019). While relative brain sizes subsequently decreased in some extinct proboscidean clades, an EQ similar to that of living elephants (and an order of magnitude higher than that of *Moeritherium*) probably characterized their ~8 Myr LCA with mammoths (Benoit *et al.*, 2019). Large brains might also have evolved convergently during the Miocene in a basal lineage that split from elephants over 30 Myr ago, the Deinotheriidae; however, detailed endocasts for this group are lacking (Benoit *et al.*, 2019; Baleka *et al.*, 2022).

As in primates and cetaceans, proboscideans attained their maximum known encephalization values late in their history, in the Pleistocene (~0.5 Myr old) Sicilian dwarf elephant *Palaeoloxodon falconeri*.



**Figure 1.** The temporal and phylogenetic distribution of maximal EQ values and likely CCE exaptations in (from top to bottom) catarrhines, platyrrhines, cetaceans, proboscideans, psittaciforms, corvids, decapods and octopods. Tree bifurcations indicate approximate divergence dates between the lineages marked by icons on the right. Tieplots show the presence of exaptations to sophonce in their respective lineages; for each lineage, maximum EQ values (Jerison, 1973) are represented by shading (legend in the top-left corner). In non-vertebrates to which EQ measures are inapplicable, branches are marked by N/A. Data from Ni et al. (2019); Montgomery et al. (2013); Benoit et al. (2019); Ksepka et al. (2020); Prum et al. (2015); Whalen and Landman (2022).

Its EQ of around 4 was anomalous for proboscideans and roughly on par with that of dolphins (Larramendi and Palombo, 2015; Lyras, 2018; Benoit et al., 2019). The degree to which the oversized brain of *P. falconeri* was tied to a minimal size threshold for brain functioning (Palombo and Giovanazzo, 2005; Larramendi and Palombo, 2015) is unclear since encephalization is by no means a universal correlate of island dwarfism (Lyras, 2018). Tantalizingly, *P. falconeri* matched humans and surpassed other elephants in its longevity and delay of sexual maturity, accommodating a long growth phase (Köhler et al., 2021). As in humans (Gould, 1985), this extended maturation phase was complemented by a paedomorphic adult morphology, with a globular and proportionally enlarged braincase (Larramendi and Palombo, 2015). Given its cerebral architecture, delayed maturation and the possibility of island settings being particularly conducive to tool use (Hansell and Ruxton, 2008; Haslam, 2013), the recently extinct *P. falconeri* might have possessed a range of CCE exaptations unmatched among proboscideans.

### Avian intelligences

Like mammals (Bertrand *et al.*, 2022), birds underwent rapid and convergent encephalization during the Cenozoic while greatly expanding their EQ range (Ksepka *et al.*, 2020). The earliest Mesozoic birds, such as the 150 Myr old *Archaeopteryx*, overlapped with their non-avian theropod ancestors in relative brain size (Balanoff *et al.*, 2013). The same holds true for members of the grade comprising ratites, fowl, grebes and pigeons – all of which diverged between the late-Cretaceous and the earliest Palaeogene around 66 Mya (Field *et al.*, 2020; Ksepka *et al.*, 2020).

Soon after the Cretaceous-Palaeogene boundary (66 Mya), a significant shift towards larger brains and smaller bodies took place at the base of the vast evolutionary radiation spawning the rest of living birds, the Neoaves (Claramunt and Cracraft, 2015; Ksepka *et al.*, 2020). Against the neoavian baseline, high encephalization evolved multiple times independently during the Cenozoic (Ksepka *et al.*, 2020). Paleoneurology and comparative neuroanatomy also suggest convergent Cenozoic increases in the size of the avian neocortex homologue known as *wulst* (Stacho *et al.*, 2020), which is involved in higher mental functions including tool use (Milner and Walsh, 2009; Tambussi *et al.*, 2015; Walsh and Knoll, 2018) but was likely absent in at least some Mesozoic stem-group birds (Beyrand *et al.*, 2019). In particular, dramatic *wulst* enlargements occurred in the parrot (Psittaciformes) and corvid (Corvidae) lineages (Walsh and Knoll, 2018), which also comprise the most encephalized of birds. Parrots and corvids reached EQs on par with those of apes (Emery and Clayton, 2004) convergently and by distinct routes: whereas parrots reduced their body sizes relative to the brain, corvid brain enlargement outpaced a parallel increase in body size, as in the case of hominin encephalization (Ksepka *et al.*, 2020).

The fossil record of corvids is fragmentary, hampering the tracking of their brain evolution. Nonetheless, the inferred timing of corvid origins based on molecular data (Jønsson *et al.*, 2016) broadly matches the age of their earliest fossil remains. These are attributed to the middle Miocene (~15 Myr ago) corvids *Miocorvus* (Milne-Edwards, 1869; Gál and Kessler, 2006) and *Miocitta* (Brodkorb, 1972), both known mainly from fragmentary limb bones. The fossils of later middle Miocene corvids, such as *Miopica*, are similarly scant (Курочкин and Соболев, 2004). However, all belong to small birds that may have been behaviourally, phenotypically and cognitively (Ksepka *et al.*, 2020) closer to other living passerines than most extant corvids. Fossils from the Pliocene onwards belong instead to morphologically and possibly cognitively modern forms (e.g. Kessler, 2013; Pavia, 2020; Nunez-Lahuerta *et al.*, 2021).

Besides primates, corvids are arguably the most plausible living precursors to sophonce. These birds display high social intelligence (Clayton *et al.*, 2007; Keefner, 2016), numerosity (Nieder, 2018), cooperative hunting and problem-solving (Seed *et al.*, 2008; Yosef and Yosef, 2010) and, tentatively, future-planning abilities (Raby *et al.*, 2007). Their physical and social cognition skills broadly match those of apes (e.g. Bird and Emery, 2009; von Bayern *et al.*, 2018; Pika *et al.*, 2020), with tentative experimental support for causal reasoning and insight (Bird and Emery, 2009; Taylor *et al.*, 2009, 2012).

A corvid, the New Caledonian crow (*Corvus moneduloides*), also possesses some of the most remarkable toolmaking traditions among animals (Hunt and Gray, 2007; Holzhaider *et al.*, 2010). In the wild, New Caledonian crows famously manufacture ‘fishing probes’ out of hooked twigs, fern branches, or *Pandanus* leaves to forage (Hunt, 1996; Hunt and Gray, 2004). New Caledonian crow toolmaking is selective (Chappell and Kacelnik, 2002), flexible (Knaebe *et al.*, 2017) and culturally transmitted (Holzhaider *et al.*, 2010). Uniquely among birds, its geographical variants hint at a degree of CCE, with stepwise modifications of an ancestral design that cannot be explained by ecological variability alone (Hunt and Gray, 2003) despite seemingly lacking the open-endedness of human CCE. This impressive toolmaking repertoire, the product of dexterous beaks that like hominin hands may have ‘coevolved’ with tools (Matsui *et al.*, 2016), shows that primate-like appendages are not a prerequisite for complex technology.

This hypothesis is corroborated by parrot tool use, which rivals that of corvids in complexity. Goffin’s cockatoos (*Cacatua goffiniana*) manufacture wedge-like, piercing and extractive tools deployed sequentially as part of a functional set. This procedurally taxing form of tool use was

previously thought to be restricted to primates (O’Hara *et al.*, 2021). In another creative instance of tool use, the omnivorous Kea (*Nestor notabilis*) of New Zealand, which shows puzzle-solving skills at least on par with those of New Caledonian crows (Auersperg *et al.*, 2011), can use sticks to deactivate baited traps (Goodman *et al.*, 2018). Complementary evidence for complex cognition in parrots comes from studies on numerosity, memory and categorization skills (Pepperberg, 2006), as well as cooperative problem-solving (Schwing *et al.*, 2016) and possibly culture (Klump *et al.*, 2021).

Given the phylogenetic spread of CCE exaptations in parrots, their origins probably trace back to the 40–30 Myr old LCA of Keas and all other living parrots (Prum *et al.*, 2015; Provost *et al.*, 2018; Selvatti *et al.*, 2022). Unfortunately, the avian fossil record is too sparse and fragmentary to track brain evolution in parrots from an Eocene passerine-like baseline (Mourer-Chauviré, 1992; Mayr and Göhlich, 2004; Worthy *et al.*, 2011; Mayr, 2015). Nonetheless, it corroborates an early-mid Cenozoic origin for their crown-group (Waterhouse, 2006).

### Cephalopod intelligence: A temporal outlier?

The phylogenetic chasm separating cephalopod molluscs and vertebrates makes complex cognition in coleoids – the clade including octopods (octopi and their close relatives) and decapods (squids and cuttlefish) – a uniquely informative case study in convergent evolution (Moroz, 2009; Vitti, 2013; Roth, 2015). The LCA of coleoids and vertebrates lacked the shared organizational features of the tripartite avian and mammalian brains (Vitti, 2013). In fact, it plausibly lacked a brain altogether (Hejnl and Martindale, 2008), considerably weakening the case for attributing the recurrent evolution of animal intelligence to shared neuroanatomical underpinnings (Lineweaver, 2009).

Coleoids are widely considered the most intelligent living invertebrates (Moroz, 2009; Vitti, 2013; Roth, 2015; Amodio *et al.*, 2019, 2020). Cuttlefish possess a sense of numerosity (Yang and Chiao, 2016) and can delay gratification to reap higher-quality future rewards, a putative invertebrate unicum (Schnell *et al.*, 2021). Octopi have been shown to solve puzzles by ‘insight’ (Richter *et al.*, 2016), possess strong memory-based navigation (Mather and O’Dor, 1991) and physical intelligence (Fiorito *et al.*, 1990; Borrelli *et al.*, 2020) and recognize both real and virtual objects (Kawashima *et al.*, 2020). Some may engage in social learning (Amodio and Fiorito, 2013). More broadly, sociality is widespread in coleoids. In decapods, it manifests along a continuum from lifelong gregariousness in squid to episodic shoaling in cuttlefish (Drerup and Cooke, 2021). While octopi have instead often been portrayed as quintessentially solitary, this is not the case for all species. For instance, gloomy octopi (*Octopus tetricus*) tolerate high densities of sedentary conspecifics, with whom they engage in multi-faceted social interactions (Scheel *et al.*, 2017).

Coleoids also display multiple variants of tool use. Several species use jets from their siphon to repel other animals or flush away objects (Mann and Patterson, 2013), including during play (Mather and Anderson, 1999). To this form of ‘liquid’ tool use, octopi add the selection and transport of objects to modify their dens (Mather, 1994) and the launch of debris to fend off conspecifics (Godfrey-Smith *et al.*, 2021). Remarkably, at least one species (*Amphioctopus marginatus*) crafts composite tools in the form of portable shelters and shows possible anticipatory behaviours by transporting them for future deployment (Finn *et al.*, 2009).

In light of their Precambrian LCA with birds and mammals, the intelligence of cephalopods has been implied to be similarly ancient and taken as an argument for the improbability of sophonice arising even in lineages possessing multiple CCE preconditions over extended timespans (Lineweaver, 2009, p. 10). If so, cephalopods would stand out as major outliers in an evolutionary landscape where intelligence is largely a Cenozoic phenomenon. However, palaeontology and comparative cognition do not support this notion.

The cerebral organization of ancestral Cambrian shelled cephalopods (Kröger *et al.*, 2011) is likely mirrored by that of *Nautilus*, as shown by outgroup comparisons (Sasaki *et al.*, 2010). The *Nautilus* brain consists of a circumesophageal ring with little internal differentiation (Shigeno *et al.*, 2008). In contrast, coleoids display the most complex nervous systems known in invertebrates (Darmaillacq *et al.*,

2014): both decapods and octopods possess elaborate, multilobed brains, adding hierarchical organization and a profusion of interconnections to their molluscan groundplan (Grasso and Basil, 2009).

The roots of coleoid cerebral complexity probably lie in the loss of their ancestral molluscan shell, which may have fostered cognitive evolution by upping predatory pressure and facilitating the exploitation of challenging, variable benthic habitats (Amodio *et al.*, 2019). In accord with this hypothesis, predatory pressure from fishes and other marine vertebrates has often been invoked as an ancient driver of coleoid cognitive evolution (Packard, 1972). These ‘shell loss’ scenarios hint at more recent origins of coleoid intelligence than may otherwise be assumed. Shell reduction and loss is a recurring theme in the post-Devonian (<360 Ma; Whalen and Landman, 2022) history of coleoids: in accord with Packard’s (1972) scenario, escalating taxonomic and ecological diversification in fishes – particularly during the mid-late Mesozoic – was accompanied by independent losses or shrinkages of mineralized skeletons in both vampyropods and decapods (Dera *et al.*, 2016; Whalen and Landman, 2022). For instance, squids probably internalized and reduced their skeletons in offshore, deepwater Mesozoic habitats; in all likelihood, their sophisticated physical intelligence and body patterning abilities evolved independently of those of other cephalopods amid a later Cenozoic re-invasion of shelf settings (Arkhipkin *et al.*, 2012; Amodio *et al.*, 2019).

If the colonization of complex shallow-water and seafloor niches was an important driver of coleoid cognitive evolution (Amodio *et al.*, 2019, 2020), this link may be most apparent in the camouflage skills and physical intelligence of the largely benthic incirrate octopi (e.g. *Octopus*; Amodio *et al.*, 2019), which possess the most elaborate multilobed brains of all cephalopods (Grasso and Basil, 2009). Similarly, benthic habits probably fostered the evolution of the elaborate camouflage and signalling repertoire of cuttlefish (Josef and Shashar, 2014). The shallow-water benthos was most likely colonized independently, and recently, by the ancestors of *Octopus* and *Sepia*: the bodyplans of early vampyropods (Fuchs *et al.*, 2007; Whalen and Landman, 2022) and stem-group decapods such as belemnites (Rowe *et al.*, 2022; Whalen and Landman, 2022) suggest a nektopelagic habit in the coleoid LCA. Since the morphology and plausible lifestyle of the earliest known Mesozoic octopi were reminiscent of free-swimming cirrates (Fuchs and Schweigert, 2018; Fuchs *et al.*, 2020) the late-Mesozoic (López-Córdova *et al.*, 2022; Whalen and Landman, 2022) LCA of living Octopoda was probably not benthic, either (Amodio *et al.*, 2019; 2020).

Independent evidence from neuroanatomy and comparative cognition also suggests that the intelligence of octopi and decapods arose partly by parallel elaborations of a simpler ancestral blueprint. MRI scans of the vampire squid *Vampyroteuthis infernalis*, the basalmost living member of the octopod lineage (Vampyropoda), have revealed a relatively small, smooth (lissencephalous) brain (Rowe *et al.*, 2022). In contrast, several lineages of coastal, partly social octopi possess cerebral lobes with complex surface convolutions. This neuroanatomical condition (gyrencephaly) is also associated with sociality and behavioural complexity in vertebrates (Rowe *et al.*, 2022).

Lissencephaly in vampire squids may hypothetically be a consequence of their derived bathypelagic lifestyle (Rowe *et al.*, 2022). However, currently available evidence suggests that it is more likely to be an ancestral condition. *Vampyroteuthis* has a cerebrotypic intermediate between decapods and octopods (Maddock and Young, 1987) and is generally considered the most plesiomorphic extant vampyropod (Whalen and Landman, 2022). Accordingly, the lissencephaly of vampire squids is shared with decapods (Chung *et al.*, 2022). These observations suggest that the complex cerebral gyres and subdivided lobes of gyrencephalous octopi are not ancestral coleoid traits but rather relatively recent cognitive specializations that probably evolved multiple times independently within octopods themselves (Chung *et al.*, 2022).

Overall, palaeontology and comparative cognition paint a picture of the coleoid LCA as an animal with an intelligence well above the molluscan baseline, but falling short of the remarkable cognitive performances of modern octopi and cuttlefish. In all likelihood, these were partly a product of the escalatory ecological dynamics of Mesozoic oceans, one that in some lineages was later elaborated upon to negotiate shallow-water and benthic niches during the Cenozoic. *Octopus*-grade brains were almost certainly not a Precambrian invention: while octopi may have split from primates nearly 600 Mya

(Lineweaver, 2009), octopus intelligence – and octopi themselves – are late-Phanerozoic novelties. As such, they offer no argument for a stagnant cognitive landscape in which sophonce is a primate fluke. What cephalopods do offer is evidence that the evolutionary paths to complex cognition are manifold: of all factors traditionally proposed to drive the evolution of mammalian and avian intelligence, only one – variable, complex niches – is shared with coleoids (Vitti, 2013).

### **Bridging the gap: Does hominization supply a rate-limiting step to N?**

Despite the phylogenetic spread of CCE exaptations, it may be proposed that it is the transition between a social, tool-using, cognitively sophisticated animal baseline and sophonce that supplies a rate-limiting step to N. This hypothesis is consistent with CCE being an evolutionary ‘singularity’ on present-day Earth. However, it arguably clashes with the tempo and mode of hominin cognitive evolution.

Hominins split from the chimpanzee lineage less than 10 Myr ago, in the late Miocene (Langergraber *et al.*, 2012). Their subsequent history was tied to technology, cultural transmission and niche construction to a degree unmatched in other primates and indeed across animals (Sterelny, 2007). The creation of this hominin ‘socio-cognitive niche’ or ‘hominization’ (Stopa, 1973; Whiten and Erdal, 2012) was accompanied by unparalleled encephalization and cerebral reorganization relative to the great ape baseline (Falk, 2012; Alatorre Warren *et al.*, 2019; Ni *et al.*, 2019; Melchionna *et al.*, 2020).

Nonetheless, the proposed drivers of the hominin cognitive escalation, including group size and complexity, toolmaking, meat-eating, food processing and terrestriality find at least partial analogues in other primates (Wynn and McGrew, 1989; Stanford, 1995, 2001; Dunbar, 2003; Visalberghi *et al.*, 2005; Ottoni and Izar, 2008; McGrew *et al.*, 2019; Dunbar and Shultz, 2021) and non-primates (Connor, 2007; Foote *et al.*, 2016; Matsui *et al.*, 2016). New World monkeys offer a case in point. While probably less cognitively demanding than early Palaeolithic stone knapping (Lombard *et al.*, 2019), lithic tool use by *Cebus* likewise entails terrestriality, extractive foraging, social learning and bipedal transport in savanna-like environments. In this respect, it echoes the earliest lithic industries of Pliocene Africa (Ottoni and Izar, 2008), which might themselves have been the product of multiple ecologically distinct hominin lineages (Plummer *et al.*, 2023). Moreover, putative Pliocene cutting tools have been found to be virtually indistinguishable from the byproducts of stone percussion by monkeys, suggesting that the lithic technologies of early *Homo* evolved by readily co-opting the products of a simple, phylogenetically widespread behaviour (Proffitt *et al.*, 2023).

After the Pliocene, parallel increases in brain size trends emerged across archaic *Homo* populations on different continents, both intra- and interspecifically (Rightmire, 2004; Shultz *et al.*, 2012). Pleistocene brain expansion culminated in the evolution of endocranial volumes above 1400 cm<sup>3</sup> in the two most encephalized species on Earth: modern humans (*H. sapiens*) and the extinct Neanderthals (*H. neanderthalensis*), which split from each other before 430 Ka (Arsuaga *et al.*, 2014). In accord with neuroanatomical findings, emerging archaeological data shows that Neanderthals shared a significant portion of the *sapiens* behavioural and techno-cultural repertoires. These hominins mastered multi-step composite manufacture (Sykes, 2015; Hardy *et al.*, 2020), specialized bone processing (Soressi *et al.*, 2013) and fire use (Allué *et al.*, 2022), with some evidence for cumulative culture (Langley *et al.*, 2008). Like modern humans, Neanderthals also produced ornaments (Zilhão *et al.*, 2010; Radović *et al.*, 2015) and possible decorative motifs (Leder *et al.*, 2021).

Whether Neanderthals would have been capable of developing a technological civilization, and could thus be considered ‘sophont’ *sensu* Wright *et al.* (2018), is unknown. What is increasingly apparent, though, is that their technical and cultural output was not fundamentally dissimilar to that of *H. sapiens* prior to its late-Pleistocene dispersal outside Africa. For instance, whereas simple nonfigurative symbols were probably produced by both Neanderthals and early African *sapiens* (Henshilwood *et al.*, 2018; Leder *et al.*, 2021), it was only around 40 000 years ago – after the ‘Out of Africa’ dispersal of our species – that representational art spread around the globe (Roebroeks and Soressi, 2016; Aubert *et al.*, 2018; Brumm *et al.*, 2021).

Together with language (Berwick and Chomsky, 2016) and religious behaviour (Bloch, 2008), representational art is unknown outside of ‘behaviourally modern’ *H. sapiens* (Aubert *et al.*, 2018; Botha, 2020). Mastery of these domains certainly appears to be a human singularity. No matter how stark and consequential, though, the cognitive gulf between the Neanderthal-*sapiens* LCA and modern humans took vanishingly little time to bridge ( $10^4$ – $10^5$  years; e.g. Arsuaga *et al.*, 2014) on a geological time-scale. In this respect, the transition to ‘behavioural modernity’ was not at all commensurate to major evolutionary transitions spaced hundreds of millions to billions ( $10^8$ – $10^9$ ) of years apart (Levin *et al.*, 2019) and stands out as an unlikely candidate among possible rate-limiting steps to N. The same holds true if the timeframe is widened to the full 5–10 Myr-long transition between the earliest hominins, which most likely possessed a spectrum of CCE exaptations matched by modern primates (Whiten *et al.*, 1999; Visalberghi *et al.*, 2005; Ottoni and Izar, 2008) and *H. sapiens* (Langergraber *et al.*, 2012).

### The Silurian hypothesis: A palaeontological test

The proliferation of CCE exaptations within the last  $10^2$  Myr of Earth’s history, and the early appearance of sophonce in their wake, raises the question of whether this time window is exceptionally favourable to the emergence of technological intelligence, or else finds analogues deeper in geological time. This question is directly relevant to the Silurian hypothesis – the notion that humans were not the first species on Earth to build a technological civilization (Schmidt and Frank, 2019). As Schmidt and Frank (2019) note, the fossil record could provide evidence for or against the existence of ‘antecedents’ – species that may ‘lead downstream to the evolution of later civilization-building species’ within a given timeframe.

As highlighted by Frank (2018), the fossil record famously captures only a small percentage of all species that ever existed (Darwin, 1859). However, it is generally adequate for tracking diversification patterns and lineage histories at the family level or above (e.g. Benton, 1995, 2009; Benton and Simms, 1995; Benton *et al.*, 2000; Tarver *et al.*, 2007; Kalmar and Currie, 2010; Sahney and Benton, 2017). In fact, for many fossil groups taxonomic richness is already approaching an asymptote as sampling increases (Benton, 2009). The quality of the fossil record at higher taxonomic levels is also not irreparably compromised as older strata are sampled, providing a surprisingly accurate window onto Phanerozoic evolution (Benton *et al.*, 2000; Sahney and Benton, 2017) and the means to test the Silurian hypothesis indirectly.

Hundreds of thousands of fossil species are known (Valentine, 1970; Alroy, 2002). Arguably, though, the number of plausible antecedents to sophonce outside the stem-groups of Cenozoic intelligences (e.g. fossil hominins or proboscideans) is virtually null. Unless the evidence for correlations between morphology and intelligence is rejected, this claim cannot be dismissed as a case of survivorship bias. In principle, it would have been possible for an indefinitely large number of extinct fossil lineages to act as starting points for evolutionary trajectories to sophonce. No proposed ‘antecedent’ (Schmidt and Frank, 2019), however, shows a buildup of the necessary exaptations.

The prototypical speculative sophont spawned by a fossil lineage is Russell and Séguin’s (1982) ‘dinosauroid’. This creature was imagined as a future descendant of troodontids, a group of small bird-like theropods possessing the highest relative brain size among dinosaurs. Troodontid EQs were roughly on par with those of ostriches, cassowaries and chicken (Balanoff *et al.*, 2013; Ksepka *et al.*, 2020). If comparative cognition is any guide, this points to cognitive skills incompatible with civilization-building. None of this indicates that dinosaurian sophonce is impossible in principle. However, troodontid encephalization and cerebral complexity were on par with those of archaic Cretaceous birds and the attainment of corvid- or parrot-grade intelligence in the avian lineage took a further tens of millions of years (Balanoff *et al.*, 2013; Ksepka *et al.*, 2020). The same applies to dinosauroid sophonce in Russell and Séguin’s (1982) alternate timeline. While late-Cretaceous troodontids may have had grasping arms and large brains relative to the reptilian baseline (Varricchio *et al.*, 2021), their short temporal range before the end-Mesozoic mass extinction and lack of any sustained encephalization or brain reorganization trends within this timeframe (Ksepka *et al.*, 2020) suggest that

no hidden transition to sophonce lurks in their fossil record. In this respect, troodontids are unremarkable compared to fossil ratites or fowl, which have never been proposed as plausible antecedents to sophonce.

The evolution of CCE preconditions in dinosaurs did eventually occur, but it was a Cenozoic phenomenon restricted to specific avian clades – far postdating the origins of birdlike dinosaurs. As such, it was decoupled from the evolution of flight (Balanoff *et al.*, 2013, 2016), and by the same token there is no reason to suspect that extinct flying reptiles were singularly intelligent (Edinger, 1948). Accordingly, endocast data suggest that pterosaur EQs fell below those of all living birds, and their large brain size relative to the reptilian baseline is mostly accounted for by large optic and cerebellar lobes for sensorimotor control (Witmer *et al.*, 2003).

Similarly, the timing of cetacean encephalization suggests that there is nothing cognitively special about secondarily aquatic vertebrates per se (Marino *et al.*, 2007; Marino, 2022). Extinct Mesozoic marine reptiles, such as the dolphin-like ichthyosaurs, are extremely unlikely candidates for dolphin-like intelligence (Edinger, 1948). Like those of pterosaurs, ichthyosaur brains had enlarged optic and cerebellar lobes for navigating their three-dimensional realm but were reptilian in size, structure and organization (Marek *et al.*, 2015). More improbable still is the notion that ichthyosaurs provided the raw materials rather than the brainpower, for manifestations of Mesozoic sophonce. Triassic ichthyosaur skeletons disassembled and turned to artwork by a sophont ‘Kraken’ (McMenamin, 2012) would offer a ‘smoking gun’ for the Silurian hypothesis. However, this proposal at once ignores far more parsimonious alternatives (Hogler, 1992; Bottjer, 2002) and conflicts with the timing of coleoid origins and key adaptations as inferred from molecular phylogenetics and the fossil record (see ‘Cephalopods’).

Could proof of ‘Silurians’ lie with an extinct clade phylogenetically closer to humans? As a hypothetical example, Frank (2018) speculated that some early mammal species might have risen to civilization and remained undetected, during the Palaeocene. The mammalian fossil record suggests otherwise. All the available evidence indicates that encephalization and cerebral complexification in mammals followed and did not precede, their Cenozoic rise to ecological prominence. Mammalian lineages experienced rapid and widespread increases in body mass in the immediate aftermath of the end-Cretaceous mass extinction, in which their dinosaurian predators and competitors had been extirpated (Bertrand *et al.*, 2022). Convergent trends towards neocortical expansion, the enlargement of cerebellar regions tied to higher cognition and encephalization (Smaers *et al.*, 2018, 2021; Bertrand *et al.*, 2022) only began gaining traction about 10 Myr later (Bertrand *et al.*, 2022). Against this backdrop, any lineage of Palaeocene mammalian sophonts would stand out as an evolutionary fluke. None does. Mammals did spawn a sophont species, but this required tens of millions of years of cumulative cognitive evolution – not a sudden Palaeocene leap forward.

More broadly, cognitive complexification in synsapsids, the group comprising mammals and their extinct relatives, is a late-Cenozoic phenomenon. On the grounds of both encephalization and brain structure, a case could be made for the late Permian (~255 Myr ago) *Kawingasaurus* being the most cognitively advanced non-mammalian synsapsid. This small, fossorial creature evolved an analogue of the mammalian neocortex independently of mammal ancestors and had an EQ triple that of other non-mammalian synsapsids (Laaß and Kaestner, 2017). However, *Kawingasaurus* was a cognitive exception in its time only. Its EQ of 0.52 would place it well below average among living mammals, and its neocortical analogue was incipient and primarily devoted to subterranean navigation (Laaß and Kaestner, 2017).

Other hypothetical foreshadows of sophonce in Permian synsapsids are similarly unexceptional when set against crown-group mammals. For instance, remotely primate-like grasping appendages and arborality manifest in the late Permian *Suminia*, an ‘anomodont’ relative of *Kawingasaurus* (Ivachnenko, 1994; Fröbisch and Reisz, 2009). However, the grasping appendages of *Suminia* were far more akin to the clinging feet of bats or birds than to dexterous primate hands (Fröbisch and Reisz, 2009). The *Suminia* braincase also displays none of the cognitive specializations of *Kawingasaurus* (Rybczynski, 2000), let alone any evidence for primate-like intelligence. Although Permian synsapsids

show sparse harbingers of the exaptations that were to foster mammalian sophonce, by all measures technological civilization was far out of their cognitive reach.

Amid this plethora of unlikely antecedents, the fact still stands: the modern biosphere offers several lineages co-expressing multiple preconditions to sophonce, virtually all of which emerged during the Cenozoic. In stark contrast, the fossil record offers no convincing ‘antecedents’ beyond the stem-groups of those same lineages. The recent and convergent origins of intelligence and other CCE preconditions, the quick appearance of sophonce in their wake and the lack of plausible analogues deeper in geological time add up to a Cenozoic cognitive ‘explosion’ (CE; Fig. 1). As for other evolutionary episodes in the history of life, possible explanations may be sought in both extrinsic, contingent environmental triggers or long-term, cumulative macroevolutionary trends.

## Explaining the Cenozoic cognitive ‘explosion’

### *‘Permissive environment’ explanations: Windows of opportunity as a limiting factor*

The onset of permissive physical conditions offers intuitively appealing explanations for key geobiological episodes. The Cambrian Explosion of animal disparity and biodiversity is often explained in terms of ocean oxygenation or other geochemical triggers (Zhang *et al.*, 2014). The rise of Carboniferous giant arthropods (Harrison *et al.*, 2010) and vertebrate flight (Dudley, 1998) has similarly been attributed to a jump in atmospheric O<sub>2</sub> and that of Cretaceous angiosperms to global warming or aridity (Zhang *et al.*, 2018). By the same token, mid-Cenozoic global cooling has been proposed as a trigger for mammalian and avian encephalization. Under this scenario, lower temperatures enhanced thermoregulation of larger, more energy-expensive brains in ‘warm-blooded’ vertebrates (Schwartzman and Middendorf, 2000).

However, the evidence for global temperatures imparting first-order control on cognitive evolution is weak at best. The evolution of intelligence and tool-use predispositions in crown-group parrots almost certainly preceded the end-Oligocene global cooling (Prum *et al.*, 2015; Ksepka *et al.*, 2020; Selvatti *et al.*, 2022) and occurred in tropical climates (Selvatti *et al.*, 2022). Primate and proboscidean encephalization similarly took place in subtropical to equatorial settings, suggesting that thermodynamic constraints did not play a significant limiting role in the process (Benoit *et al.*, 2019; Ni *et al.*, 2019). Accordingly, highly encephalized species are more common in warm climates (Russell and Billingham, 1981). Contra Schwartzman and Middendorf (2000), intelligence is also not restricted to endothermic, homeothermic vertebrates and its origins in coleoids may well predate terminal Oligocene cooling (López-Córdova *et al.*, 2022; Whalen and Landman, 2022). Other contingent effects of the Palaeogene-Neogene transition, such as aridification, faunal change or increased habitat variability (Benoit *et al.*, 2019; Smaers *et al.*, 2021), may figure among the drivers of encephalization in particular lineages, including primates and proboscideans. However, these environmental factors are neither geologically unprecedented nor universally pertinent across ecological and phylogenetic divides and as such they can only offer proximate, clade-specific explanations.

Alternative ‘abiotic’ explanations for Cenozoic cognitive evolution push back the rise of permissive factors to the ~66 Myr old end-Cretaceous mass extinction. Milner and Walsh (2009) proposed that the greater brain size and complexity of crown-group birds gave them an edge over their Mesozoic relatives in the aftermath of global ecological collapse at the Cretaceous-Palaeogene boundary. However, sustained increases in both avian and mammalian cerebral complexity and the origins of modern encephalization levels postdate the end-Cretaceous mass extinction by tens of millions of years (Ksepka *et al.*, 2020; Bertrand *et al.*, 2022).

More broadly, it is increasingly apparent that the drivers of intelligence in primates, cetaceans, elephants and birds, not to mention cephalopods, are as disparate as their bodyplans and lifestyles (e.g. Seed *et al.*, 2008; Sayol *et al.*, 2016; Benoit *et al.*, 2019; Amodio *et al.*, 2020). As such, they cannot be readily subsumed under a single, external causal trigger. The only common denominator may be a complex social or physical environment (Amodio *et al.*, 2020) – a backdrop at once

singularly vague and at least as old as the Phanerozoic itself (Plotnick *et al.*, 2010; Darroch *et al.*, 2018; Hsieh *et al.*, 2022).

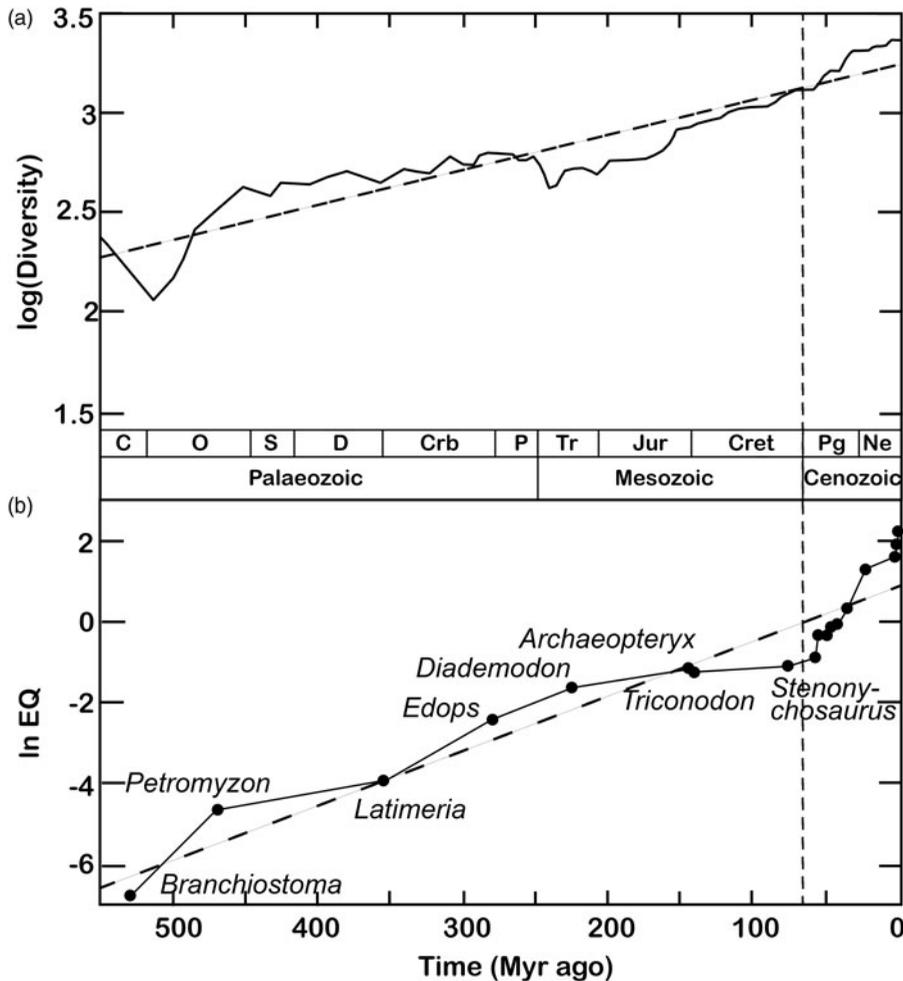
### *The ‘open world’ explanation: Time as a limiting factor*

Amid a lack of convincing, all-encompassing environmental ‘triggers’ for the CE, a simpler explanation may be offered by null hypotheses of evolutionary dynamics. The default option is that of a ‘random walk’ or ‘diffusion’ model (McShea, 1994; Marcot and McShea, 2007; Bogonovich, 2011; Rospars, 2013), in which evolving lineages explore a spectrum of values stochastically over time. In this framework, the selective pressures acting on cognitive evolution can be treated as a black box: that is, increases and decreases in intelligence can be framed as equally probable for any given lineage at any given time. Given a bounded lower limit for intelligence or a proxy of choice (e.g. EQ = 0 in the case of encephalization) and an unbounded upper limit, both mean and range (and hence maximal values) will tend to increase over time (Bogonovich, 2011). If a minimal intelligence baseline (or a minimum set of cumulated CCE exaptations) are required for sophonce to evolve, the number of lineages overshooting this requisite threshold will positively correlate with the time elapsed since the start of the ‘walk’. The more lineages participate in the random walk, the more statistically robust this emerging trend will be.

In principle, diffusion may provide the most elegant and parsimonious explanation for the Phanerozoic increase in the number of intelligent lineages: no selective pressures or other extrinsic causal drivers are required. High intelligence simply becomes increasingly common as cognitive and behavioural possibilities are passively ‘invaded’ over time and – for any given rate of change – time is the only limiting factor to the ‘filling up’ of evolutionary possibilities. The widening ranges and accompanying increases in maximal values observed for the EQs of well-studied vertebrates, including primates, cetaceans and birds, qualitatively match the predictions of the diffusion hypothesis. However, the Phanerozoic increases in maximum encephalization and behavioural complexity across Metazoa are best described by exponential functions, deviating from diffusion-based predictions (Meyer, 1954; Russell, 1983; Rospars, 2010). Accordingly, quantitative models suggest that diffusion may be insufficient to account for the exponential rise of Phanerozoic intelligence (Bogonovich, 2011) as described by Russell (1983): a ‘steepening’ or compounding factor may be required.

A largely overlooked but closer correspondence with the Phanerozoic increase in maximal intelligence may be found in global species richness curves (Fig. 2). The increase in global biodiversity over the last 540 Myr has been proposed to conform to logistic (Sepkoski, 1984) rather than exponential (Benton, 1995) functions. Accordingly, the exponential biodiversification patterns emerging from fossil tabulations (Benton, 1995) have been interpreted as artefacts of palaeogeographical sampling biases (e.g. Close *et al.*, 2020a, 2020b). However, recent spatially explicit simulations suggest otherwise. Against the expectations of logistic models, regional diversity appears mostly governed by an exponential growth regime throughout the Phanerozoic (Cermeño *et al.*, 2022). Global deviations from exponential biodiversification may be largely due to episodic perturbations such as mass extinctions and the obliteration of biodiversity hotspots by plate tectonics rather than ecological saturation capping species numbers (Cermeño *et al.*, 2022). If a carrying capacity to Earth’s species richness exists, it may be so high as to have had virtually no effect on global diversification rates since the origins of complex multicellularity. This open-endedness is reflected at finer spatial and temporal scales by the results of recent biological invasions and ecological experiments (Harmon and Harrison, 2015).

If exponential biodiversification is factored into a ‘random walk’ model, the number of participating lineages deviates from constancy. Instead, it increases nonlinearly over time – mirroring and potentially underlying, the escalation of Phanerozoic intelligence (Fig. 2). If so, the Cenozoic CE may need no special explanation. Instead, it may simply have emerged through cognitive ‘diffusion’ compounded by an exponential increase in the overall number of lineages alive at any given time – and, as a consequence, of the number of ‘trials’ available for diffusion to tap into intelligence at any given time. Given an exponentially diversifying biosphere, the frequency of cognitive or behavioural ‘extremes’



**Figure 2.** Classic plots of biodiversity and encephalization values through geological time. (a) The diversification of complex life through the Phanerozoic, plotted as logarithm of family-level richness for all organisms, terrestrial and marine (maximum curve). Redrawn from Benton (1995). (b) The non-linear increase in maximum encephalization quotient (EQ) levels during the Phanerozoic. The 'living fossils' Branchiostoma, Petromyzon and Latimeria serve as proxies for the maximum level of encephalization at various intervals of the Palaeozoic, based on phylogenetic bracketing and resemblance to extinct taxa. Cenozoic data points (taxon names not shown) include Plesiadapis, Tetonius, Heptodon, Homacodon, Necrolemur, Leontinia, Argyroctetus, Homo habilis, H. erectus and H. sapiens. The regression line (dashed) follows the equation  $\ln EQ = 0.0135 \times (531 - t) - 6.23$ . Redrawn from Russell (1983). In both diagrams, the vertical dashed line marks the beginning of a sharp Cenozoic uptick in both diversity and maximum encephalization levels. Legend: C, Cambrian; O, Ordovician; S, Silurian; Crb, Carboniferous; P, Permian; Tr, Triassic; Jur, Jurassic; Cret, Cretaceous; Pg, Palaeogene; Ne, Neogene.

past a given threshold of interest will likewise increase nonlinearly. Under this model, higher biodiversity simply begets a wider envelope of biological outcomes and preconditions to sophonce are no exceptions. Vice versa, a special explanation for the CE would be required under a logistic biodiversification paradigm. Given null conditions of time invariance in the mean and distribution of intelligence and constant global species richness, the sampling biases imposed by a winnowed fossil record deeper

in time (e.g. Close *et al.*, 2020a, 2020b) stand out as insufficient to explain the consistent clustering of intelligence proxies towards the lower extremes of their present-day distributions (Jerison, 1973, 1994; Russell, 1983; Rospars, 2010; Bogonovich, 2011; Smaers *et al.*, 2018, 2021; Ksepka *et al.*, 2020; Stacho *et al.*, 2020; Bertrand *et al.*, 2022).

Furthermore, against the predictions of logistic models, exponential biodiversification may be ecologically self-reinforcing. Adaptive radiations not only tend to show little evidence of slowdowns over time (Benton and Emerson, 2007; Harmon and Harrison, 2015) but may compound speciation rates themselves by precipitating finer ecological partitioning (Emerson and Kolm, 2005). More species create more variegated selective pressures to face and expand the range of opportunities for other taxa to ‘diversify into’ (Benton and Emerson, 2007). The rise of flowering plants – angiosperms – during the late Mesozoic and early Cenozoic is a case in point (Benton *et al.*, 2022). The hypothesis that the boost in terrestrial primary productivity precipitated by the angiosperm radiation fostered the evolution of energetically expensive large brains, facilitating the evolution of complex cognition (Bogonovich, 2011), may be especially pertinent to land-dwelling mammals and birds. If so, angiosperms provide a prime example of how Phanerozoic biodiversification prepared the ground for its own further exploration of biological (and cognitive) possibilities. Like other manifestations of biological complexity (e.g. Cailleux, 1976; Ball, 1985), intelligence appears to have escalated by hitchhiking on such compounded diversification, in an ‘open world’ where no upper ceiling to its frequency or overall abundance exists. No causal driver unique to the CE may be required to explain this occurrence, which appears to be a robust emergent feature of Phanerozoic macroevolution.

A shared feature of economic, technological and cultural innovation as well as biology, the open-ended exploration and simultaneous creation of adjacent possibilities stands out as a universal hallmark of evolving systems (Kauffman, 2019). The self-sustaining and amplifying evolutionary dynamics emerging as a result are most likely not a fluke of Earthly biology (Cortês *et al.*, 2022). Crucially, though, Phanerozoic-style biospheres harbouring complex, animal-grade multicellularity will be bound to the open-ended creation of evolutionary and ecological novelty to a degree unmatched in purely microbial biospheres, as attested by the fossil record (Butterfield, 2007, 2011). The reasons for this are grounded in the physics of scale and motion.

The size and motility of animals enable them to mechanically engineer their environments, disrupting isotropy in time and space through bioturbation, fluid advection and selective resource harvesting (Butterfield, 2011, 2018; Budd and Jensen, 2017). Moreover, the macroscopic size of animals imposes a degree of biogeographical provinciality unsustainable in microbes, where chances for allopatric speciation are greatly diminished by long-range dispersal and astronomical population sizes (Norris, 2000; Butterfield, 2007). Pervasive ecosystem engineering and predation by animals further boost biotic heterogeneity by extending ‘arms races’ and other coevolutionary dynamics to macroscopic life and by structuring complex multi-tiered food webs (Butterfield, 2000, 2007, 2011). At the same time, the combinatorial ontogenetic potential of their differentiated cell and tissue types (Marshall, 2006; Butterfield, 2007) translates into a virtually open-ended range of behaviour and morphologies. Above all, animals are key arbiters of global biomass supplies and their partitioning. Since longevity and size tend to positively covary across organisms, an animal-dominated biosphere is one where standing biomass stocks are multiplied relative to a microbial world, with no extra primary productivity needed (Butterfield, 2007); and in both biological and nonbiological evolving systems, when supply rates of raw materials and energy are boosted opportunities for innovation and diversification increase (Vermeij, 1995).

Although their precise course will be modulated by contingencies, the histories of extraterrestrial biospheres harbouring animal-grade multicellularity can thus be expected to unfold along similar lines to Phanerozoic Earth (Butterfield, 2007) on account of first-principles physics and basic evolutionary rules. Arguments for contingency (Gould, 1990) fail to account for the consistent rebound of Phanerozoic exponential diversification in the face of unpredictable mass extinction events (Cermeño *et al.*, 2022): far from underpinning the rise of sophonce, such improbable geological contingencies temporarily perturbed an exploratory process bound to tap into it.

### CE drivers and model choice

An ‘open world’ scenario of cognitive evolution in Phanerozoic-style biospheres has repercussions on the choice of models used to estimate ETI abundance. Evolutionary scenarios centred on geobiological contingencies, such as the chance onset of key innovations or permissive conditions, are most amenable to ‘step modelling’. Under this framework the path to sophonce passes through a series of unlikely events, their probabilities kept low and constant over time (Bogonovich, 2011). That is, step-based models assume that once a step has taken place the next occurs at a constant average rate (e.g. Snyder-Beattie *et al.*, 2021). A CE grounded in exponential evolution undermines this assumption. It points to the probability of sophonce emerging being highly nonuniform across the Phanerozoic, with a strong positive skew towards the present. Accordingly, the marked temporal clustering of animal intelligences and CCE preconditions contrasts with the dispersed timing of major evolutionary transitions, the traditional targets of step models (Hanson, 1998; Watson, 2008; Snyder-Beattie *et al.*, 2021). Regardless of the applicability of step-based frameworks to major evolutionary transitions (e.g. Snyder-Beattie *et al.*, 2021), this strongly suggests that ‘long-fuse’ alternatives based on continuous, incremental evolutionary models (Bogonovich, 2011) and entailing a gradual increase in the probability of sophonce arising may best describe the protracted, cumulative ‘minor transition’ from animal-grade multicellularity to sophonce. Sophonce may require a long time to evolve not because it depends on an astronomically unlikely roll of dice, but because its evolution is limited by the supply rate of evolutionary novelty and rests upon an incremental increase – an evolutionary ‘buildup’ – in probability.

A long fuse model may nonetheless be approximated by a step-based alternative in which the origins of CCE exaptations represent discrete ‘minor steps’ distinct from the origin of sophonce. In this framework where sophonce is ‘deconstructed’ into its enabling steps, the multiple origins of intelligence and other CCE preconditions from a tissue-grade metazoan baseline could be factored in, rather than lost in the black box of the singular origin of sophonce. Instead of being treated as a singular improbable step, the transition from complex multicellularity to sophonce could thus be decomposed into a sequence of cumulative (and arguably far less improbable) enabling events. This approach could help refine likelihood estimates for the evolution of ETI, potentially leading to an upward revision of N compared to recent works (e.g. Snyder-Beattie *et al.*, 2021). Such a revision would take into account that the appearance of social, cognitively sophisticated, tool-using lineages among animals required over 500 Myr (Dunn *et al.*, 2018, 2021) but occurred minimally 8 times within the last  $10^2$  – in coleoids, parrots, corvids, proboscideans, cetaceans, hominoids, cercopithecoids and New World monkeys. The final substep in the evolution of sophonce on Earth – the eventual appearance of CCE itself among these lineages – occurred only once (in hominoids), but required an order of magnitude less time (Langergraber *et al.*, 2012).

From a frequentist standpoint, the repeated origins of tool-using social intelligences suggest that their evolution among metazoans is not exceedingly unlikely in the Phanerozoic biosphere. The long timescale required for their emergence does not invalidate this argument: instead, it underscores the cumulative nature of cognitive evolution in the Phanerozoic world, in which time and the supply of evolutionary novelties – and not the onset of permissive geobiological conditions – are the key limiting factors. The transition from social, tool-using intelligence to sophonce was instead a ‘singularity’, but one that occurred extremely rapidly on a geological timescale and well in advance of complex life’s ultimate demise (Cavosie *et al.*, 2005; Franck *et al.*, 2006). While anthropic self-selection bias and the low probabilities of major evolutionary transitions (Snyder-Beattie *et al.*, 2021) may explain why sophonce appeared late in Earth’s habitable timeline (at ~4300 out of ~6000 Myr; Cavosie *et al.*, 2005; Franck *et al.*, 2006), they may not account as readily for its much earlier origin relative to the estimated total lifespans of animal-grade multicellularity (after ~580 out of ~1780 Myr; Franck *et al.*, 2006; Pu *et al.*, 2016) or social, tool-using animal intelligences (after ~100 Myr or less out of a potential ~1300; Franck *et al.*, 2006). Whether animal intelligence and human sophonce differ in ‘degree’ (Darwin, 1871) or ‘kind’ (Wallace, 1869), this suggests that the crossing of the

‘behaviourally modern’ (Sterelny, 2011) human Rubicon was almost certainly not commensurate to eukaryogenesis, the evolution of complex multicellularity, or even abiogenesis (Snyder-Beattie *et al.*, 2021) in its improbability.

### SETI and the future of terrestrial intelligence

Taken together, the recurrent evolution of animal intelligences and the early apparition of sophonce in its wake suggest that  $f_s$  is likely not a significant limiting factor to the number of detectable ETIs. This opens the door to a universe in which biospheres shaped by animal-grade organisms will likely spawn sophonce on a timescale commensurate with the duration of the Phanerozoic.

All else being equal, under an ‘open world’ scenario an  $f_s$  value approaching 1 also implies that the temporal density or ‘permanence’ of sophonce should rise nonlinearly as biospheres age. Barring a major reversal of Phanerozoic biodiversification dynamics or strong negative (e.g. competitive) feedbacks, on macroevolutionary grounds the average number of antecedents to sophonce (Frank, 2018) available at any given time is set to increase in a similarly exponential fashion. Therefore, the likelihood of sophonce emerging in any given interval will also tend to escalate over time. Given a constant average lifetime for each sophont species, it follows that the ‘interregna’ between one and the next will tend to become shorter and sparser as a function of biosphere age. In contrast, instances of temporal overlap will tend to increase in frequency. The same general tendency towards a higher temporal permanence of sophonce would emerge naturally even in a simple (i.e. non-compounded) diffusion-based scenario (e.g. Bogonovich, 2011, fig. 2): in an exponentially diversifying biosphere it is merely accelerated.

In both simple and compounded diffusion scenarios, the unlikelihood of ‘Silurians’ is thus mirrored by a nonlinearly increasing probability of sophonts in the planet’s deep future. Against this backdrop, on purely macroevolutionary grounds humans are unlikely to be the last sophonts to arise on Earth. EQs on par or above those of the earliest hominins, and a comparable range of CCE preconditions, occur in living cetaceans (Marino, 2017), corvids and parrots (Emery and Clayton, 2004; Ksepka *et al.*, 2020), apes and monkeys (e.g. Ni *et al.*, 2019). If the history of the human lineage is any guide, in principle all could attain sophonce within the next  $10^1$  Myr. If the timeframe is expanded by an order of magnitude to  $10^2$  Myr, the potential ancestors of sophont species multiply dramatically: complex brains and EQs well above those of any known  $10^2$  Myr old vertebrate are widespread in dozens of extant lineages (e.g. Ksepka *et al.*, 2020; Bertrand *et al.*, 2022). This  $10^2$  Myr window would still be shorter than the estimated remaining lifespan of complex multicellularity by one order of magnitude (Franck *et al.*, 2006). Against arguments for contingency (Gould, 1990; see Ćirković, 2007), *H. sapiens* may hypothetically sit at the cusp of a new phase in Earth history, in which sophonce becomes a frequent and recurrent feature of the biosphere.

Under such a scenario where  $f_s \approx 1$ , it is the evolutionary transitions upstream of the origins of animal-grade multicellularity that would impose the strictest limits on ETI frequency. Eukaryogenesis, abiogenesis and sexual reproduction are all plausible bottlenecks or ‘hard steps’ (Levin *et al.*, 2019; Snyder-Beattie *et al.*, 2021). Nonetheless, Bayesian estimates of ETI’s likelihood based on step models (Snyder-Beattie *et al.*, 2021) indicate that increasing biosphere lifetimes to match those offered by long-lived red dwarf systems yields high probabilities of achieving these major evolutionary transitions. If  $f_s \approx 1$  and the stellar environments of red dwarfs are not inherently hostile to complex life (Gale and Wandel, 2017), the ubiquity of sophonts may thus be virtually guaranteed. If they are not (e.g. Barnes *et al.*, 2013), even under  $f_s \approx 1$  we may indeed, to a first approximation, be alone. Under both scenarios, focusing search for extraterrestrial intelligence (SETI) efforts on ancient red dwarf systems may offer one of the most useful tests of ETI’s likelihood. If habitable planets several times older than Earth are devoid of ETIs, sophonce could indeed be an evolutionary fluke. If they are not, a solution to the Fermi paradox (Ćirković, 2018b) would be at hand. In either case, the information payoff could arguably be greater than for any other stellar environment.

An ‘open world’ scenario of cognitive evolution is also pertinent to more exploratory research programmes in the SETI. If  $f_s \approx 1$ , the discovery of any animal-grade organism outside Earth would imply

that sophonce should be widespread in the galaxy. ‘Martian trilobites’ (Conway Morris, 2018) or European macrofauna (Chyba and Phillips, 2001) would dramatically raise the success chances of high-impact, high-risk efforts including space archaeology in the solar system (Villarreal *et al.*, 2022) or the search for non-terrestrial artefacts within Earth’s atmosphere (Siraj *et al.*, 2022). Should these fail, a stronger focus on possible roadblocks to ETI detection *after* the origination of sophonce would be justified. If sophonce is readily evolvable, but nowhere to be seen, the Fermi Paradox stands out as all the more puzzling (Conway Morris, 2011, 2018).

## Conclusion

When questioned about the existence of ETI, Drake (2006) expressed an optimistic take based on Earth’s fossil record, portraying the evolution of humanlike minds as a virtually inevitable outcome of natural selection. The history of intelligence on Earth suggests that Drake was right, but for the wrong reasons. The cognitive preconditions to sophonce may be far from universally adaptive, and yet they arose frequently and foreseeably as the exponential diversification of Phanerozoic life expanded the gamut of possibilities. Treating the transition from animal-grade multicellularity to sophonce as a discrete ‘singularity’ overlooks its incremental nature and the fact that most of its unlikely substeps have indeed aligned on the same evolutionary lineage multiple times. The origins of complex brains, sociality, culture and technology are all among them. If sophonce is exceptionally difficult to evolve from a metazoan-grade baseline, it is the origin of any putative human unicum that must supply the rate-limiting factor to its frequency. In the context of a sample size of 1, this possibility should not be dismissed altogether. However, the pace and timing of human evolution against the backdrop of the multiple origins of animal intelligence suggests that it is an unlikely one. Earth’s history suggests instead that the transition between animal-grade multicellularity and sophonce is not a rate-limiting step in the emergence of technological civilization and that the frequency of sophonce may be constrained primarily by earlier evolutionary ‘bottlenecks’. If biospheres exist around long-lived red dwarf stars, where sufficient time is available for these bottlenecks to be overcome, sophonce may be virtually ubiquitous. Whether this is the case or not, the lifespan of Earth’s carbon cycle still allows for no less than 800 and up to 1200 Myr of complex multicellularity. Our own sophont lineage arose from a widespread cognitive and behavioural baseline in less than 10. If intelligence is a ‘child of time’ (Tchaikovsky, 2018), plenty is left for surprises.

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