Research Article

The Role of Carbon Dioxide in the Evolution of Intelligence: Solving the Dinosauroid Question

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In this paper, I propose that the appearance of highly encephalized species on Earth during the past ca. 50 million years, and in particular the rapid encephalization of hominins during the past few million years, was favored by low CO_2 concentrations and high O_2/CO_2 ratios in the atmosphere. This hypothesis is based on the high metabolic cost of the brain in multicellular creatures that requires not only a high oxygenation rate, but also an efficient removal of CO_2 from tissues. Hence, the low atmospheric CO_2 concentrations of the late Cenozoic Era could have generated large brains with a high neuron density, including the human one.

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1. Introduction

The evolutionary origin of intelligence was discussed perhaps for the first time by Charles Darwin in his *The Descent of Man* (1871). After more than one century and a half, the issue is far from being fully understood, and studies and discussions continue to appear in the scientific literature. In 1982 by Dale Russel and Ron Séguin [1] argued that a Dinosaur species of the late Cretaceous, the *Stenonychosaurus Inequalis*, could have evolved into a humanoid-shaped sentient species; the "dinosauroid." The question of why that never happened, and why it took hundreds of millions of years for sentient species to appear on Earth, is a long-standing puzzle. In this paper, I propose that the evolution of large, complex brains is directly linked to low CO_2 atmospheric concentrations and the consequent high atmospheric O_2/CO_2. This condition was uniquely favorable for brain oxygenation during the late phases of the Cenozoic Era.

The possible role of CO_2 in the evolution of intelligence was noted first by Schwarzman and Middendorf [2], [3] and later re-proposed by Kleidon [4]. According to their interpretation, a cool environment facilitates heat dispersion and makes it possible to maintain large brains. Here, I suggest that the effect on intelligence is only in part related to temperature, but mostly to the biochemical effects of CO_2 on the metabolic system of aerobic organisms. In particular, I propose that the atmospheric O_2/CO_2 ratio is a fundamental parameter determining the oxygenation of the brain and hence its metabolic activity. The importance of this ratio has been emphasized by Buxton in a recent paper [5].

This interpretation is compatible with the paleo data on Earth's temperature and atmospheric composition. While the O_2 concentration remained approximately constant or slightly declined during the Cenozoic Era, the CO_2 concentration strongly declined. This decline and the associated increase in the O_2/CO_2 ratio went in parallel with the radiation of highly encephalized and socially collaborative mammals and birds [6]. During the last few million years, in the Pleistocene Epoch, the O_2/CO_2 ratio reached possibly the highest values ever experienced by the ecosystem during the whole Phanerozoic Eon. It was during this time that highly encephalized hominins, and eventually the homo sapiens species, appeared. If a high O_2/CO_2 ratio is necessary for the development of intelligence, then we can understand why Dinosaurs never evolved into intelligent species and why Russell's "dinosauroid" remained a thought experiment. With the high CO_2 levels typical of the Mesozoic Era, they were never able to oxygenate large brains at the required level to make them an evolutionary advantage.

If correct, this hypothesis has relevant consequences for the future of humankind. It highlights the need to eliminate human-caused CO_2 emissions as fast as possible, not just to avoid global warming but also to avoid long-term damage to the human brain. It is also relevant to the management of future habitats where humans would live for a long time, such as in space or on Mars. This hypothesis also suggests that intelligent carbon-based life is more likely to be found on exoplanets with a high O_2/CO_2 ratio in the atmosphere.

2. The Evolution of Intelligence

Intelligence leaves no traces in the fossil record, but the size and the shape of ancient brains can be recovered using endocasts. The allometric relationship between brain and body size was discovered by Jerison in the 1970s [6]. From this relation, it is possible to determine the "encephalization quotient" (EQ), which describes the deviation of the size of the brain of a certain species from the expected value

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calculated for its clade. The value of the EQ depends on the choice of the clade, and sometimes the term PEQ (Phylogenetic, or Progressive, Encephalization Quotient) is used to refer to a specific subclade. For instance, modern humans have an EQ equal to ca. 7-8 if measured with respect to all mammals, but only around 2-3, if measured with respect to the hominin clade.

The encephalization quotient alone is insufficient to describe the actual cognitive abilities of living beings. It has been argued that the absolute brain size is a better metric, at least among some clades [7]. Additionally, the neuron density in brains may vary, so that the cognitive ability can be much different even for the same EQ [8]. This problem, and the lack of extensive data, creates a substantial uncertainty in the quantification of the development of intelligence over the history of life on Earth. However, it has been recognized for a long time that a trend toward larger brains, and hence higher cognitive abilities, exists for vertebrates throughout the Phanerozoic Eon.

The earliest traces of animals endowed with brains go back to the Cambrian Period, approximately 520 million years ago [9]. During the Paleozoic Era (539-252 Ma ago), brain sizes and EQs increased over time for the dominant land clades: the synapsids and the sauropsids. The following era, the Mesozoic (252-66 Ma ago), saw the rise of reptiles, dinosaurs, and early mammals. Dinosaurs eventually developed relatively brainy taxa such as the Troodontidae, which lived about 75 My ago [10]. The *Stenonychosaurus Inequalis*, the species studied by Russell and Séguin, was closely related to the Troodonts, although it is debated whether it was actually one [11]. It is speculated that these dinosaurs could have an intelligence comparable to that of some modern birds [12]. We also have evidence that some dinosaurs could show social behavior in terms of herding, pack hunting, and family groups; an indication of relatively high cognitive abilities [13]. Recently, Herculano-Houzel suggested that some theropods, such as the Tyrannosaurus Rex, could have had a level of intelligence comparable to that of modern primates [14], but this interpretation may have been optimistic [15]. In general, dinosaurs had small brain volumes and EQs in comparison to modern mammals [16]. Note also that many dinosaurs developed long necks, even carnivorous ones such as the Troodontidae. A long neck may be useful for locating prey, but it is a disadvantage in terms of having to oxygenate the brain by pumping blood all the way from the heart. It is hard to think that these long necks could be compatible with large brains and high intelligence.

The great mass extinction at the K-Pg (Cretaceous-Paleogene) boundary (66 Ma ago) wiped out the non-avian dinosaurs and led mammals and birds to occupy their ecological niches. The result involved an initial growth of body sizes not followed by a corresponding allometric increase of brain size [17]. The

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trend reversed after the temperature peak called "PETM" (Paleocene-Eocene Thermal Maximum), about 55 million years ago. From then on, both mammals [17] and birds [18] underwent an increase in their encephalization quotient and their sociality [19]. Hominins marked a further burst of higher encephalization. They appeared during the late Cenozoic, 4-5 million years ago, and the modern Homo Sapiens some 300,000 years ago [20].

Not only did brains increase in size during the late Cenozoic, but several species developed brains that pack a higher neuron density than the average mammal in the frontal cortex [21]. This high density does not pertain to human beings only, but to a variety of non-human species, including some primates and mammals such as raccoons, and birds (corvids and parrots) [22], [23], [8], [21]. Humans may also be exceptional in having a special gene that codes for high neuron density [24].

This long and complex story encompasses more than half a billion years and raises several questions. Natural selection knows no such thing as "manifest destiny," it only selects what works. If an organism develops a large brain, it must be because its returns in terms of fitness overcome its higher metabolic cost. But why do we see a long-term trend toward higher encephalization?

The discussion on this subject has generated several interpretations, not necessarily mutually exclusive, but in most cases not completely explaining the observations. The simplest approach is based on a traditional interpretation of Darwinian natural selection, seen as gradual and slow. In this case, high intelligence took a long time to emerge because Earth's biota had to slowly "climb Mount Improbable" as Richard Dawkins referred to the concept of fitness landscape in 1996 [25]. Dale Russel was thinking in these terms about his dinosauroid hypothesis, proposing that it would have needed several tens of millions of years to develop human-level intelligence, something that couldn't happen because of the end-Cretaceous catastrophe.

Today, however, it is generally recognized that evolution moves in bursts. It is "punctuated" as it was defined by Eldredge and Gould [26]. This is especially true about adapting an existing organ to a different purpose than its original one ("exaptation" [27]). An often cited example is the peacock's tail, discussed by Ronald Fisher in 1930 [28]. It is an evolutionary positive feedback process that today takes the name of "Fisherian Runaway Selection" or "Runaway Selection." Originally, the peacock's tail was just a tail, but then it became a sexual signaling organ for males.

Runaway selection has often been invoked to explain the rapid appearance of human intelligence, since it took no more than ca. 4-5 million years to evolve from the early hominins to the modern *homo sapiens*. In

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most cases, the proposed answer involves the need for large brains to support the social and technological abilities of hominins. For instance, large brains led to the capability of mastering fire and using it for cooking. That led to a lower need for heavy jaws and metabolically expensive digestive systems. That, in turn, left free some metabolic energy to develop even larger brains in a classic runaway feedback process. This interpretation was proposed first by Richard Wrangham in his *Catching Fire: How Cooking Made Us Human* (2009), and described also by Suzana Herculano-Houzel [21]. In general, large brains are believed to be subject to the Fisherian runaway selection not just about cooking, but in relation to social and technological abilities [19].

These theories are valid accounts of how the encephalization process can bootstrap itself to reach high levels. But they don't explain why the mechanism that led to human brains was triggered up only during the past few million years and not earlier in the ca. 350 million years of existence of tetrapods on land. A different approach takes into account that evolution does not just involve adaptation to a static environment, but it is the result of a dynamic interaction of the biosphere, the atmosphere, and the geosphere [29]. The question is, then, what factor that favored high encephalization was present during the second part of the Cenozoic, and even more during the Pleistocene, but not, for instance, during the Mesozoic at the time of the Stenonychosaurus?

Considering that brains are metabolically expensive organs, this question can be related to the factor that led to the appearance of land vertebrates and vascular plants during the Paleozoic: free oxygen at high concentrations in the atmosphere. Yet, this parameter remained constant or slowly declined during the Cenozoic, so it cannot explain the encephalization. Conversely, in 2000, Schwarzman and Middendorf [2], [3] identified an alternative geophysical factor: the cooling effect of low CO_2 concentrations during the late Cenozoic. Low temperatures make it easier to disperse heat and hence cool large brains. Later, Kleidon explored the same concept [4].

The hypothesis based on climate cooling is certainly valid, but it runs into a fundamental problem. Earth is a big planet, and temperatures vary widely across different latitudes and altitudes. If a cold climate were the necessary ingredient for the development of intelligence, it would be possible to find it in Boreal regions or at the top of mountains. For instance, the region that now forms Australia had a temperate climate and hosted several dinosaur species during the Mesozoic. But there is no evidence that it hosted especially encephalized species – for instance, no troodontid remains were found there. Hominins, then, appeared in the tropical regions of central Africa, and not in the colder boreal regions.

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In the present paper, I expand the interpretation based on low CO_2 concentrations, but I propose a different mechanism for its functioning: the metabolic effect that favors the oxygenation of brain tissues for high O_2/CO_2 ratios. This factor does not depend on latitude or altitude; all aerobic creatures living on Earth's surface breathe the same air and are subjected to the same biochemical effects.

3. Atmospheric Composition and Brain Metabolism

Brains are energy-hungry machines, and that's especially true for large ones. For instance, the human brain consumes about 20% of the body's metabolic energy flow at rest [30]. Sustaining the activity of a large and densely packed brain is possible only by means of high metabolic rates. In aerobic creatures, these high rates are generated by the oxidation of glucose (or ketones) to produce metabolic energy in the form of ATP (adenosine triphosphate) as the energy carrier. The reaction involves multiple steps, but it can be written in a simplified form. The opposite reaction, photosynthesis, closes the biosphere cycle by reacting CO_2 with H_2O to reform O_2 and organic compounds.

$$O_2 + CH_2O \rightarrow CO_2 + H_2O + \text{energy}.$$

The metabolic oxidation of glucose is thermodynamically downhill (exergetic), that is, it is spontaneous since it occurs with an increase in entropy. As a consequence of Le Chatelier's principle, the reaction is expected to go faster for higher oxygen concentrations, but to be slowed by carbon dioxide not being transported away from the reaction site. Experimental evidence on single-celled organisms shows that this interpretation is qualitatively correct. Already in 1933, Coyne [31] showed that high CO2 concentration inhibited bacterial growth. More recent studies confirmed the effect on aerobic microorganisms [32], [33].

In microorganisms, the exchange of oxygen and carbon dioxide with the atmosphere is a relatively simple process, since it occurs through the cellular membrane. But the process is enormously more complicated in multicellular creatures ("metazoa") where the body tissues are not directly in contact with the atmosphere. Most metazoa use a two-stage process. A system of open tubes ("tracheae") carries external air inside the body to reach the "alveoli," where gases are exchanged with a water-based fluid ("blood") that transports oxygen deep into the tissues. The same fluid carries carbon dioxide back to the alveoli to be dispersed into the atmosphere.

The circulatory system of metazoa appeared during the rapid radiation of new body plans that started during the Devonian, about 350 million years ago. It involved several remarkable evolutionary innovations, including the capability of using blood to transport molecular oxygen, which is poorly soluble in water-based liquids. Mammals, reptiles, and birds all use different forms of the organic molecule called hemoglobin, which can bind up to four oxygen molecules. This molecule moves in blood while contained in specialized cells called "red blood cells" or "erythrocytes."

Hemoglobin reacts with oxygen according to an autocatalytic mechanism known as the "Bohr Effect" that causes it to saturate its bonding sites for a critical value of oxygen concentration. The oxygen-bonded hemoglobin must also "know" when to unload oxygen where it is needed. That's triggered by an allosteric transition to a non-binding oxygen state catalyzed by CO_2. Hemoglobin can also transport carbon dioxide when it is not bonded to oxygen, although the largest fraction is dissolved in blood in the form of bicarbonate ions, HCO_2^+. The release of gaseous CO_2 from hemoglobin at the alveoli is triggered by oxygen absorption and is called the "Haldane Effect." These processes regulate the oxygen supply to the body tissues.

The supply of oxygen and the removal of carbon dioxide are critical factors for the functioning of the brain. One problem is that the brain must be compact and approximately spherical in order to ensure fast communication among neurons. That leaves no space for local oxygen storage, such as using myoglobin, as it can be done in muscular tissue. As a result, the brain can survive only for a few seconds without a flow of oxygen [5].

But it is not just the lack of oxygen that damages the brain. High concentrations of CO_2 in the arterial blood can also hamper the metabolic function of the neuronal tissues. It is a normal effect of muscular and neuronal activity and the human body and that of most metazoa is equipped with internal chemical receptors which sense the CO_2 increase. The result is an increase in the respiration rate ("ventilation") to pump more oxygen into the blood and vent CO_2 out. At the same time, arteries swell in diameter to increase the flow of blood to the brain. These mechanisms tend to restore the O_2/CO_2 ratio in the brain and rebalance the ATP/ADP ratio that powers the functioning of neurons [5], [34], [35], [36], [37]. The body can also respond by restoring the blood's pH balance [38]. The kidneys increase the re-absorption of bicarbonate ions from the urine back into the blood, and also increase the excretion of hydrogen ions (H^+). As a last resort, the dissolution in the blood of calcium ions from bones provides a mechanism for buffering chronic acidity.

Nevertheless, the balancing mechanism has limits. It is known that carbon dioxide becomes lethal for atmospheric concentrations of the order of 5% (50,000 ppm) [39]. At these levels, death ensues not just because CO_2 displaces oxygen in the air, but because of the drop in blood pH and the poisoning of the brain. The result may be loss of consciousness, confusion, convulsions, and eventually, coma, respiratory arrest, and cardiovascular collapse. It is rare for living creatures to encounter such conditions, and it is probably for this reason that animals don't have sensors to detect the external CO_2 concentration. But high CO_2 levels can be generated in closed environments (e.g., mines, submarines, etc.). In some cases, they occur as natural phenomena as in the case of the Nyos lake disaster, in 2001. A burst of CO_2 coming from the lake killed almost 1800 people living nearby [40].

CO_2 concentrations higher than the current atmospheric level (ca. 420 ppm), but below a few thousand ppm (0.1%-0.5%), are not reported to cause acute poisoning effects. Nevertheless, these levels have measurable chronic health effects [41]. In the range of 1000-2000 ppm, effects include headaches, fatigue, and daytime sleepiness. In more severe cases, they involve disorientation, confusion, and memory problems. Physiological effects include raised blood pressure, type II diabetes, cardiac problems, and more. Reduced cognitive effects can be observed already at external partial pressures of 600-1000 ppm, only slightly larger than the current atmospheric concentration (ca. 420 ppm) and commonly experienced indoors [41]. Nothing is known about the effect of lifetime exposure to these concentrations, commonly encountered indoors by human beings. Even the current atmospheric level of 420 ppm (and growing), was never experienced by human beings throughout their evolutionary history. As a further element of evidence, burrowers (fossorial species), such as the African mole rat and others, tend to have a low encephalization quotients, possibly related to the low O_2/CO_2 ratio in the air they breathe [42], [43].

Modeling the health effects of CO_2 is challenging because of the complexity of the gas transport mechanism in the circulatory system. Concentrations of 1000-2000 ppm (0.1%-0.2%) are small in comparison to the alveolar CO_2 concentration, typically of the order of 5% in volume. So, these changes are normally neglected when modeling at the basic level the gas exchange using the alveolar equation [44]. Nevertheless, the gas exchange at the blood/air interface of the alveoli is determined by Henry's Law, which states that the amount of dissolved gas in a liquid is directly proportional to its partial pressure in the gas. Hence, even a small increase of the atmospheric CO2 concentration must necessarily result in a higher concentration in the blood.

Recently, Buxton developed a detailed model that estimates tissue concentrations of O_2 and CO_2 based on measurable parameters like cerebral blood flow (CBF), cerebral metabolic rate of O_2 (CMRO2), and arterial blood gases [5]. This model is highly relevant to the present discussion, even though it was not directly applied to CO_2 effects at pressures know to cause chronic health problems. The model is based on the idea that the energy gained from oxidizing glucose is used to power the thermodynamically uphill synthesis of ATP from ADP. The net entropy change ($\Delta S_{net} = \Delta S_{ox} + \Delta S_{atp}$) must be positive for the process to continue. Experiments by Wilson et al. [45] showed that the ATP/ADP ratio in the brain begins to degrade at an O_2 tissue pressure PO_2 of 12 Torr. Since normal brain tissue pressure of O_2 is only ca. 25 Torr, the safety margin is small.

Buxton proposes that it's not just low O_2 that degrades ΔS_{ox}, but a low ratio of O_2 to CO_2 concentrations. A fall in this ratio reduces the available entropy from oxidation, forcing a compensatory fall in the ATP/ADP ratio to keep the net process going, thereby impairing energy metabolism. The reaction rate is governed by the associated entropy change which, in turn, depends on the cube of the ratio of oxygen concentration to that of carbon dioxide.

It would be out of scope, here, to go into the details of Buxton's calculations. In addition, it appears that at present we don't have sufficient data for a quantitative modeling of the chronic effects of CO_2. Nevertheless, it is worth noting that the estimated impact of an atmospheric CO_2 pressure (PCO_2) going from ca. 400 ppm ($PCO_2 \approx 0.3$ Torr in inspired air) to 1000-2000 ppm (0.1-0.2%) corresponds to an inspired PCO_2 rise of ~0.7-1.4 Torr. In these conditions, the arterial pressure ($PaCO_2$) could increase by a similar amount from its baseline level (ca. 40 Torr), or ca. 1.75-3.5%. All other things remaining equal, this value does not exceed the safe limits (about a factor of 2) reported by Buxton [5] and Wilson [45]. Theoretically, the brain should continue to function in these conditions, and the real-world data show that it does. Nevertheless, the data also shows that its metabolism will slow down or suffer other negative effects. That may occur, either as a direct lowering of the oxidation potential, or because of the metabolic cost to compensate the change.

These considerations show how oxygenation and carbon dioxide removal may be important factors in determining the capability of the body of tetrapods to oxygenate large brains. Hence, it is possible to propose that large brains can be developed by natural selection only for atmospheric compositions that allow a high tissue oxygenation, that is high O_2/CO_2 ratios or, equivalently, low CO_2 concentrations when the O_2 level remains approximately constant. This factor may have been important during the late Cenozoic, and, in particular, for the evolution of hominins during the Pleistocene. Tentatively, we may assume that the difficulty of providing sufficiently high oxygen flow and removing CO_2 fast enough from the brain prevented the Fisherian runaway process that could have led to a Troodontid dinosaur, such as the Stenonychosaurus, to develop human-level intelligence in a few million years.

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The next section reviews whether this proposal is compatible with the data on atmospheric composition during Earth's history.

4. Atmospheric composition over the Phanerozoic

Aerobic life could appear on Earth only when there existed free oxygen available in the atmosphere. The "Great Oxygenation Event" (GOE), approximately 2.4 billion years ago, marked the point at which oxygen appeared, although in small concentrations. Much later, at the beginning of the Phanerozoic Eon that started ca. 541 million years ago, the oxygen concentration gradually rose to levels over 20%. These levels could sustain the high metabolic rates necessary for the evolution of large multicellular creatures endowed with brains.

In the figure, you can see recent results by Mill's *et al.* for the oxygen concentration during the Phanerozoic Eon [46]. This graph is defined as the "consensus curve" based on the results of several different measurement methods. The scale is in PAL (present atmospheric level).

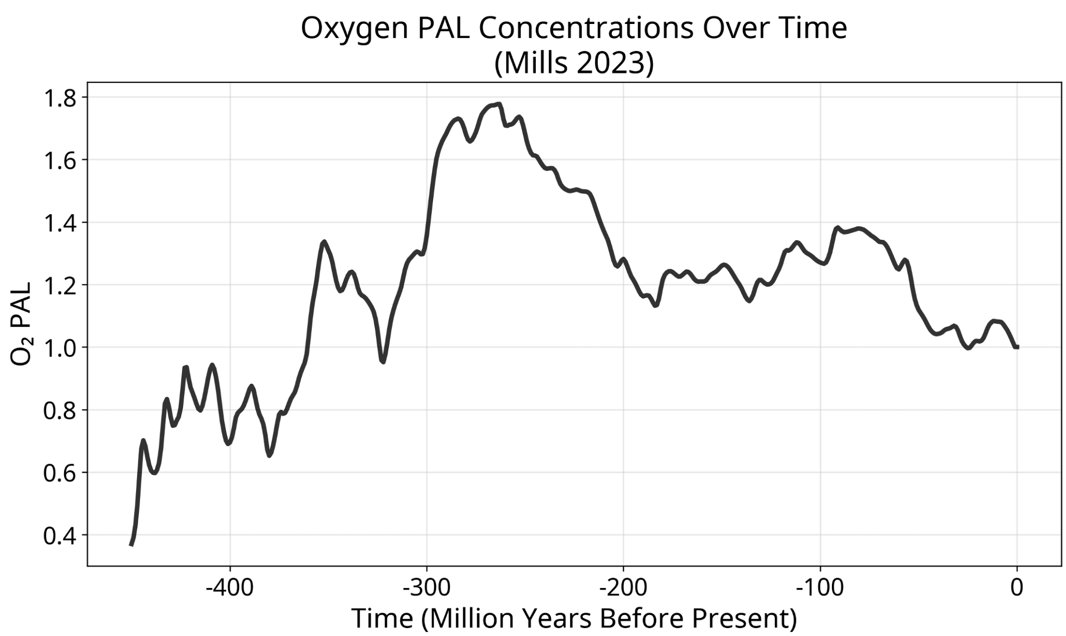

Figure 1. *The "Consensus Curve" proposed by Mills et. Al. In 2023 for the oxygen atmospheric concentration during the Phanerozoic Eon.* [46]*. The data were sourced from fig. 6 of Mills' paper using Automeris.io' "WebPlot" automatic data extraction software. Concentrations are in fractions of the present atmospheric level (PAL) assumed to be 21%*

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The oxygenation burst during the Devonian, starting about 350 My ago, is believed to have been generated by plants colonizing the continental lands, although a recent study finds a correlation with Earth's magnetic field [47]. Plants removed CO_2 from the atmosphere, and also increased the erosion rate of the land by rain, providing nutrients to the marine biota, which also absorbed CO_2. The peak at ca. -270 My appears less prominent in recent reconstruction [46], [48], more prominent in earlier ones [49], [50]. All reconstructions show that the O_2 concentration during the Cenozoic times was not especially large. Evidently, high oxygen levels alone cannot be an explanation for the late Cenozoic burst of brain power.

The CO_2 concentration showed a different trend. Figure 2 shows the data available from a recent paper by Judd *et al.* [51]. Similar results were obtained for the Cenozoic only [52]. In this case, the PAL was assumed to be the concentration before the industrial age, that is, 280 ppm. An overall decline ensued after the high values of the early Phanerozoic, followed by a relatively constant value during the Mesozoic. A further decline was observed during the Cenozoic. CO_2 concentration reached an absolute minimum during the Pleistocene, during the past few million years. Low values were also detected for the Carboniferous Period, but not as low as during the Pleistocene. Note also the recent inversion of the tendency, generated by human-made CO_2 emissions.

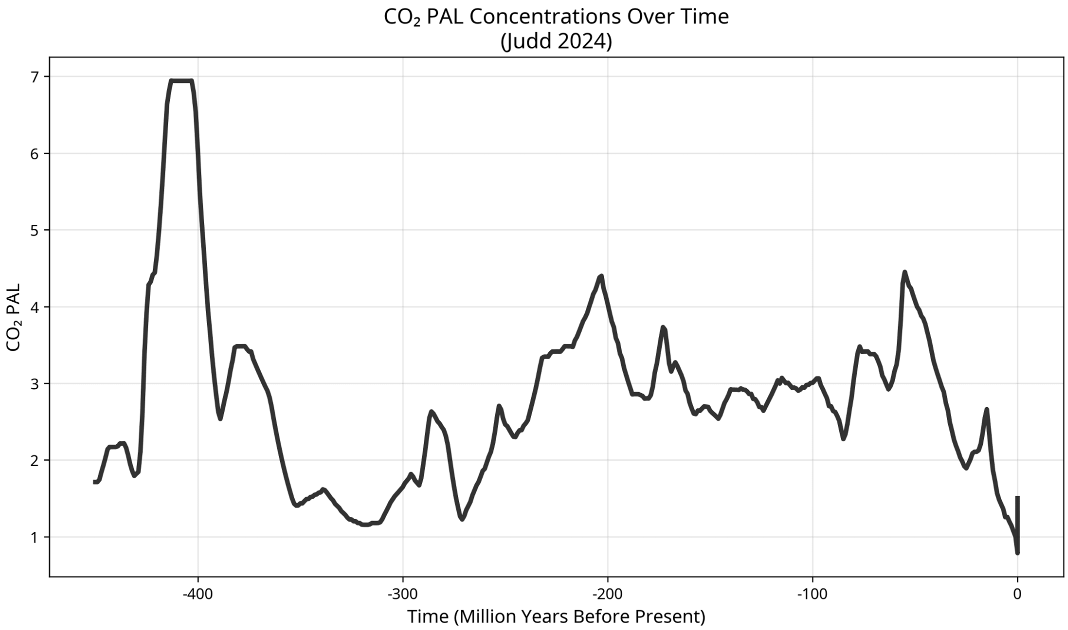

Figure 2. *Concentration of Carbon Dioxide over most of the Phanerozoic Eon. Values are in PAL (present atmospheric concentration) assumed to be equal to one for the pre-industrial value of 280 ppmv. The data have been sourced by digitizing figure 4 in the 2024 paper by Judd et al.* [51] *using the Automeris.io' "Webplot" tool. The most recent data for the Pleistocene Epoch have been sourced from the paper by Da et al.* [53]*. The current value of ca. 420 ppm is sourced from IPCC data.*

The strong oscillations in the CO_2 concentration are believed to be generated by the interaction of biological and geological factors. The outgassing of CO2 from the mantle tends to be balanced by biological factors that store carbon into inert compounds and favor the silicate erosion reaction that generates solid carbonates. The O_2 /CO_2 PAL ratio is shown in the following figure for the two data sets shown before.

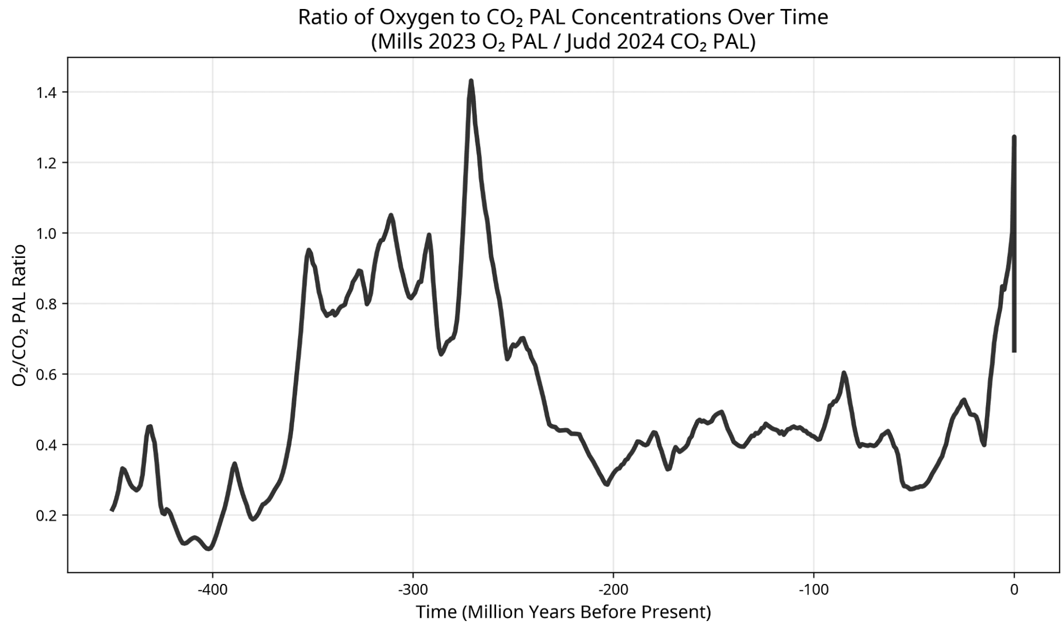

Figure 3. *O_2/CO_2 PAL ratio throughout the Phanerozoic. Data for CO_2 from Judd et al.* [51] *and for O_2 from Mills et al.* [46]*. The data were sourced as described in the previous figures.*

To evaluate the uncertainty in this data, I performed the same analysis using the dataset for O_2 and CO_2 provided by Lenton *et al.*, based on the COPSE model [48].

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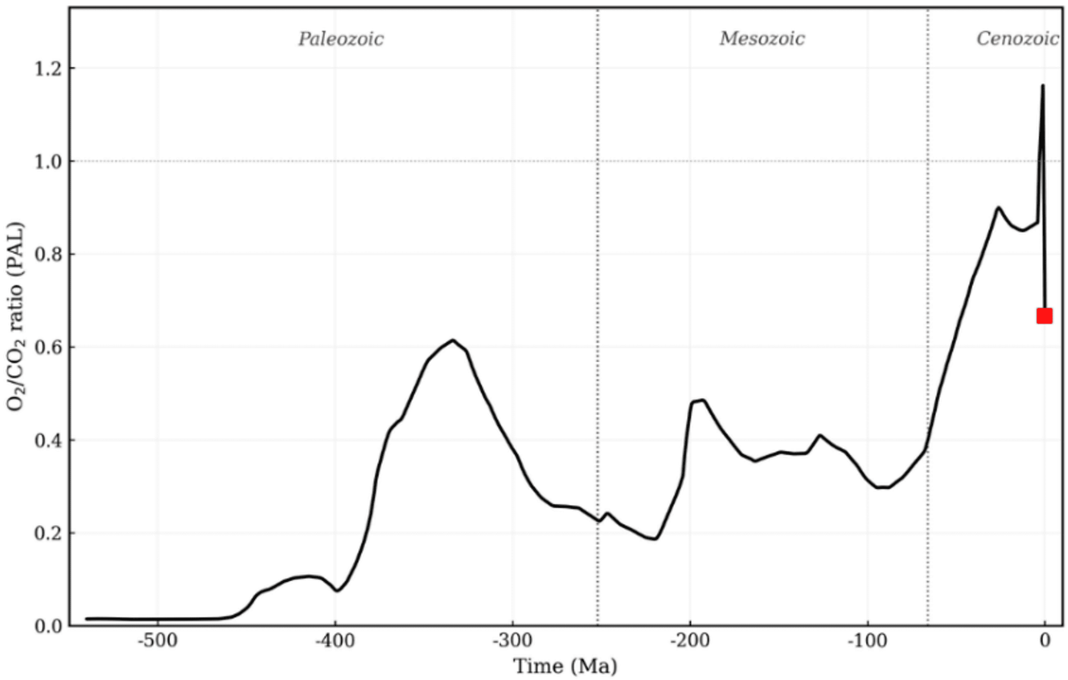

Figure 4. *Another reconstruction of the Ratio of O_2/CO_2 atmospheric concentrations across the Phanerozoic Eon. Data sourced from of Lenton et al,* [48]*, and from* [54]*,* [55]*, and* [53] *for the latest 3 million years. Values are in fractions of PAL (present atmospheric concentration) assumed to correspond to the preindustrial value of 280 ppmv of CO_2. The square dot on the right corresponds to the current value (2025) of 420 ppmv of CO_2 and 21% O_2.*

The two plots are similar, but the second one does not show the high peak of the O_2/CO_2 ratio at 271 My, which is prominent in the first. This peak may be an artifact created by the uncertainty in the measurements. Conversely, if it is a real feature of the system, then it may be associated with the evolutionary leaps of the late Paleozoic, which involved the development of new features and body plans in vertebrates.

The O_2/CO_2 ratio declined in the latest phases of the Paleozoic, probably as a result of the events that preceded the End-Permian mass extinction at 252 Ma b.p., generated by the large igneous province (LIP) known as the “Siberian Traps.” There followed the Mesozoic Era, which never reached high levels for the O_2/CO_2 ratio. The LIP called “Deccan Traps” put an end to the Mesozoic and to the non-avian dinosaurs, 66 Ma b.p. The following era, the Cenozoic, started with a phase of low O_2/CO_2 atmospheric ratio during most of the Paleogene. The trend was reversed after the start of the Eocene, with a gradual increase of the ratio that reached the highest values during the Pleistocene. Very recently, human agricultural and industrial activities reversed the trend again.

Quantifying the correlation between encephalization and the O_2/CO_2 ratio is a complex and difficult task because of the limited data available and the uncertainty in both the reconstruction of the ancient atmospheric composition and the measurements of the cerebral characteristics of ancient species. The prominent O_2/CO_2 ratio peak of the late Paleozoic does not appear to be associated with especially intelligent lifeforms. On the other hand, it is also true that the fossil record for that period is sparse, and it has been argued that if highly intelligent species existed during such a remote past, they would be extremely difficult to detect (the "Silurian Hypothesis" [56].) More likely, the still inefficient circulatory system of the tetrapods of that time, based on 3-chambered hearts, was unable to oxygenate and de-carbonize large brains. More efficient 4-chambered hearts appear to have been developed only during the early Triassic in mammals and dinosaurs.

About the Cenozoic, Bertrand *et al*. [17] report some quantitative data for encephalization during the early phases of the era. Unfortunately, these data overlap only in part with the phase of rapid growth of the O_2/CO_2 ratio of the later Cenozoic. Nevertheless, the relatively low encephalization they report for the early Cenozoic is consistent with the low O_2/CO_2 ratios in the atmosphere of the time. More data are available for the recent burst in hominin intelligence during the past few million years and the corresponding rise of the O_2/CO_2 ratio.

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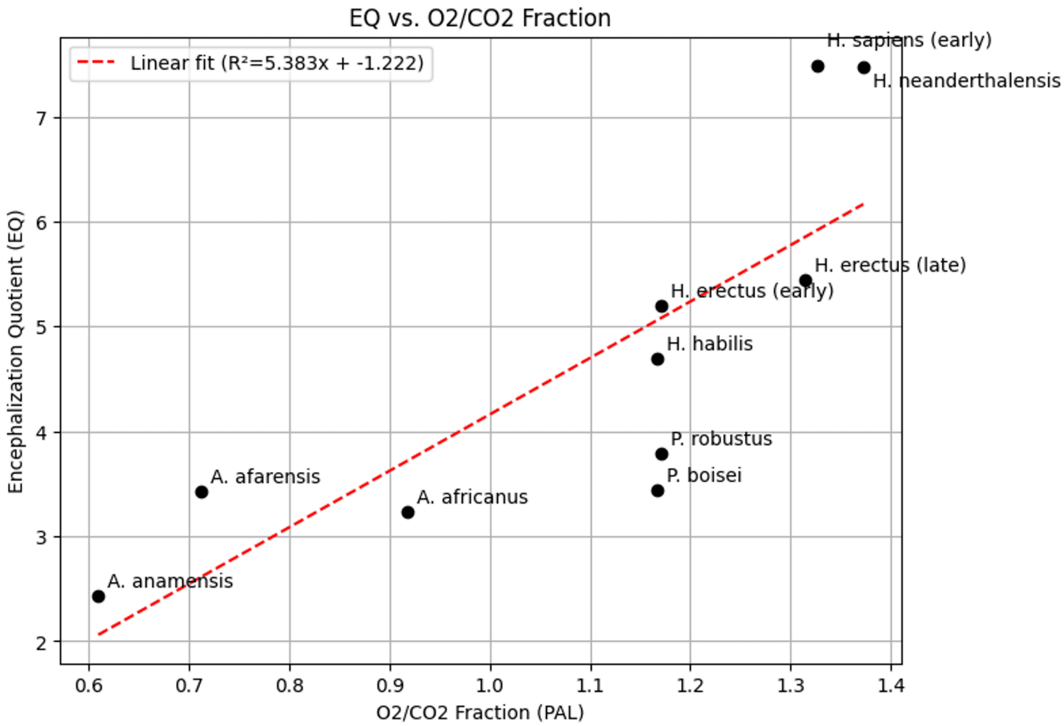

Figure 5. *Illustrative correlation between hominin encephalization quotient (EQ) and atmospheric O_2/CO_2 ratio in PAL units (Present atmospheric pressure, PAL=1) over 4.2 million years of evolution. Dashed line shows linear regression fit. Note that some species from the 1.8-2.0 Ma period (P. boisei, P. robustus, H. habilis, H. erectus early) are assigned identical atmospheric values due to limited data resolution. Denisovans and. The O_2/CO_2 fraction was estimated by smoothing the data reported by Kohler* [57]*. See "Methods" for a detailed description.*

In the figure, modern Homo sapiens was excluded to focus on evolutionary trajectory under natural atmospheric conditions. Homo floresiensis and Homo Naledi were excluded because of the paucity of data, and also considering these species subjected to island dwarfism.

These data have to be considered as illustrative only. We do not expect a linear relationship between the O_2/CO_2 ratio and the hominin encephalization. But the fact that a correlation exists supports the hypothesis that atmospheric O_2/CO_2 ratio may have played an important role in enabling the cognitive evolution in the hominin lineage.

5. Discussion

Evolution cannot be reproduced in the laboratory, so it may never be possible to prove that the high O_2/CO_2 ratio of the Pleistocene was the crucial factor that led to the development of the human brain and,

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earlier on, of the Cenozoic encephalization burst. Yet, the record of the atmospheric composition over geological time is compatible with this hypothesis, which also agrees with what we know of how the human metabolism is affected by the O_2/CO_2 ratio. Note also that this interpretation does not exclude the possible effect of atmospheric temperatures on the cooling of large brains [2], [4], nor negate the feedback effects related to social and technological factors. However, it adds a new dimension to our understanding of the development of intelligence in the biosphere: the need of efficient oxygenation of the brain in conditions of low atmospheric carbon dioxide.

If true, this hypothesis has important consequences for humankind's future. Human activities have reversed the long-term trend of CO_2 concentration decrease which had been ongoing for at least 50 million years, and that has resulted in the present concentration of about 420 ppm, nearly twice the average during the Pleistocene, when the homo sapiens species evolved. The current O_2/CO_2 ratio has now declined to levels encountered several million years ago, when modern humans did not exist. We may speculate that the current atmospheric composition may send evolution in "reverse mode," making the metabolic requirements of the large brains developed during the Pleistocene impossible to maintain.

It is also possible to speculate that his effect may have been at play with the increase in CO_2 concentration from ca 180 ppm to 280 ppm with the end of the last ice age. This change was accompanied by a significant reduction in the homo sapiens' cranial capacity [58], although the effect may also be explained by other factors [59]. More recently, the increase in CO_2 concentrations of the industrial age may explain the "reverse Flynn effect" (also known as "global dumbing"), the decline of human intelligence observed in recent years [60]. Again, there are alternative explanations based, for instance, on social factors or chemical pollution [61]. In both cases, however, it is remarkable how the increase in CO_2 atmospheric concentration goes in parallel with a reduction in the cognitive capabilities of the human brain.

These considerations need to be taken into account when discussing a possible colonization of Mars, or the occupation of large artificial space habitats [62]. The O_2/CO_2 ratio is a parameter that will need to be carefully taken into account to create an environment where humans can live for a long time and reproduce. We need to consider also the consequences in exobiology and for the search for intelligent life on exoplanets. It is an area where James Lovelock noted first the necessity of oxygen in the atmosphere of a planet for it to contain advanced lifeforms. [63], [64]. Based on the results presented here, a high O_2/CO_2 ratio in an extrasolar planet may indicate the possible presence of highly intelligent species. The possibility of determining CO_2 in extra-solar planets has been recently demonstrated on ROXs-42B b [65], [66]. A CO_2 concentration of ca. 3,400 ppm was observed. There is no evidence of the presence of oxygen in this giant planet, nevertheless this result indicates that this kind of examination is possible.

A final consideration is related to the remote future of the biosphere. The current atmospheric perturbation in terms of CO_2 emissions caused by human beings is destined to be fully reabsorbed by natural geochemical cycles in times of the order of millions of years [67]. Afterward, the Earth system will resume the long-term trend of decline in CO_2 concentrations resulting from the response of the biosphere to the slow increase of the solar irradiation, about 10% every billion years [68]. Some recent results by Ozaki and Reinhard [69] confirm these early results and show that, while oxygen is expected to remain at the current concentrations for the long term future, carbon dioxide is expected to continue its gradual decline, reaching values of the order of 10 ppm in ca. one billion years. Even at these low values, it will be possible for plants to operate the photosynthetic process using the "C4" mechanism [70]. We may speculate that in a remote future, fast tissue oxygenation in animals could generate even more highly encephalized creatures than the current ones. The evolution of highly intelligent biological creatures on Earth may have just started.

6. Conclusion

The questions examined in the present paper are enormously complex and I have no pretense to have been able to provide a definitive or unique answer. It is clear that further research and modeling will be needed to understand the relevance of the ideas presented here. Nevertheless, I thought that it was important to present a hypothesis that, to the best of my knowledge has not been explicitly expressed in the scientific literature so far. If the atmospheric O_2/CO_2 ratio is really a critical factor in the cognitive abilities of vertebrates' brains, the consequence is that it is vitally important to reduce the human perturbation on the atmospheric composition as fast as possible. Not only do we need to reduce human-generated emissions as fast as possible, but we need to reduce CO_2 atmospheric concentrations to the levels that made it possible for the "homo sapiens" species to evolve and subsist. Active CO_2 removal from the atmosphere may be necessary for the survival of the human species and the whole biosphere.

7. Methods

In figure 5, Atmospheric O_2/CO_2 ratios are expressed in Present Atmospheric Level (PAL) units, where PAL = 1.0 corresponds to pre-industrial atmospheric composition (CO_2 = 280 ppm, O_2 = 21%). The atmospheric CO_2 data was obtained from the reconstruction by Kohler [57] based on boron isotopes, smoothing the data shown in fig S13 in the supplemental material. Atmospheric Oxygen concentration was assumed to have remained at PAL=1 during the whole period considered.

The analysis includes 10 hominin species representing the main evolutionary lineage: Australopithecus anamensis (4.2 Ma), A. afarensis (3.5 Ma), A. africanus (2.8 Ma), Paranthropus boisei (2.0 Ma), P. robustus (1.8 Ma), Homo habilis (2.0 Ma), H. erectus early (1.8 Ma), H. erectus late (0.5 Ma), H. neanderthalensis (0.15 Ma), and H. sapiens early (0.2 Ma).. the encephalization quotients (EQ) are calculated using Jerison's formula (EQ = brain_mass / (0.12 × body_mass^0.67)) from fossil cranial capacity measurements and estimated body masses compiled from multiple paleontological studies [71], [72], [73], [74].

Figure 6. *Dale Russell with a model of his "dinosauroid." ca. 1980s. Photo Credit, Canadian Museum of Nature.*

Statements and Declarations

Conflicts of interest

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Disclaimer

No part of the text was written by artificial intelligence, although the work benefited from revision, criticism, data search, and elaboration by Grok 3, Gemini, Kimi, and Manus.

Data availability

All data sets reported here have been sourced from the scientific literature. The sets used for the plots are available upon request (ugo.bardi@gmail.com).

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I wish to dedicate this paper to the memory of Dale Russell (1937-2019), creator of the 'dinosauroid' concept. I had the privilege of personally meeting him in the 1980s and we found that we shared a deep passion for all things dinosaurian. It is from that encounter that I have been thinking about the "dinosauroid question" and I believe I now know a possible answer.

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