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Phylogenetic Evidence for the Early Origin of the Homeostatic Influence of the Biota on Planetary-Scale Geophysical Processes

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Abstract

This paper uses empirical evidence to address the subject of when and how Gaia arose. To set the scene for this, the paper first proposes two core necessary attributes for Gaia: each individual having control systems and joint action of groups of such individuals producing results that are more beneficial to the group than would have arisen from the isolated action of each individual. We make the case that the predominantly recognised “planetary” nature of Gaia is a contingent rather than necessary attribute. The paper next identifies representative examples in contemporary organisms of each of the two core attributes of Gaia in operation. For each of these examples, genes making up part of the genetic specification of the example were identified. We then sought these same genes in the earliest examples of life that have been genetically characterised in empirical terms - the Last Universal Common Ancestor (LUCA) and the Last Bacterial Common Ancestor (LBCA). These arose respectively between 4 and 3.5 billion years ago. Examining both the pools of known modern genes and demonstrated LUCA and/or LBCA genes, sufficient relevant modern genes were also found in LBCA and/or LUCA to provide empirical evidence that the core attributes of Gaia were present in LBCA and/or LUCA. Hence, we claim that the first Gaia likewise arose between 3.5 to 4 billion years ago. The paper also provides case studies showing similar results at increasing scales of organismal aggregation over the intervening period to the present. Dawkins (1982), defining Gaia as was predominantly done then in terms of its planetary attribute which posits that there is *one* Gaia on Earth, pointed out that neo-Darwinian natural selection requires competition between *multiple* units of selection. Given the absence of such multiple units of selection, Dawkins proposed that Gaia could not come into being by neo-Darwinian natural selection and therefore did not exist. The present study provides evidence that Gaia can exist at a range of scales greatly below planet level and that genes for the core attributes of Gaia have been available at these lower scales from near the start of life. With such genes being units of selection, planetary Gaia can come about by a series of developments commencing near the start of life, each involving standard gene-based Darwinian natural selection. We consider these results to resolve the issue raised by Dawkins (1982). The two core attributes of Gaia in operation together at the first cellular stage of life would mean that at this stage the cell had a degree of control over both its interior components and its response to its external environment. This can be seen to mean that the first successful cell was a “Gaia”, using the core attribute definition. Therefore, from at least as early as LUCA to the present, every configuration of cells - first into biofilms, then into multicellular organisms and on up to the

> most modern and the largest – can be seen as a combination of smaller Gaias. This process can be seen to continue up to the level of the involvement of the whole biosphere. This gives us Gaia at planetary scale, the concept first presented to science by Lovelock (1972), some fifty years ago.

Keywords: Phylogenetics, Origin, Homeostasis, Biota.

Significance

This paper identifies genes in modern organisms that are part of the specification of each of the two core attributes of modern Gaia. Sufficient of these modern genes were also found from phylogenetics in LBCA and/or LUCA. These results provide empirical evidence that the core attributes of Gaia were present in LBCA and/or LUCA. Hence, we claim that the first Gaia likewise arose between 3.5 to 4 billion years ago.

1. Introduction

A considerable number of studies provide evidence of homeostatic influences from the biota to geophysical processes at planetary scale. These studies span a period of time from Lovelock (1972) to the present (for example, Leggett and Ball, 2021). Since Lovelock (1972), studies involving this concept have referred to the object of the research as Gaia and we also do so in this paper (also see Appendix 1).

The present paper is an investigation into when and how the homeostatic influence of the biota on planetary-scale geophysical processes – Gaia - originated.

There are several dimensions to this question: time (both modern and ancient), the physical attributes of Gaia (morphology – both present and fossil), and genetics (present and ancient via phylogenetics).

To commence the study, we first seek the necessary as opposed to contingent attributes (Kment, 2021) of Gaia – those that are present in all as opposed to some cases of Gaia.

Having specified such necessary attributes – and nominating two as “core”, we then find genes for functions that exemplify these attributes in present-day organisms. We next turn to phylogenomics, the comparative study of the entire genetic complements of different species (Chan and Ragan, 2013).

In the work utilising phylogenomics, we are greatly aided by the evidence that many of life’s present systems evolved early: there is evidence of the existence of unicellular life up to 4 billion years ago (Ga) (Betts et al., 2018) which in multiple ways is similar to extant unicellular life (Weiss et al., 2016; Coleman et al., 2021). Hence, many genes seen in modern life are also seen in early life. This pool of such genes gives us a chance to characterise a biological process in current life, find genes for it, and then see if those genes were also present in life near its start.

From phylogenomics, we utilised two further findings. The first is that the more widely across all living things the same gene is seen, the earlier in the history of life the gene originated (Weiss et al., 2016). The second is that, with the use of appropriate phylogenomic techniques, one can infer that if a modern gene has a role in a cell function, and that same gene is present in very early life, then that gene had the same role in early life and that the same cell function existed then (Eisen, 1998; Weiss et al., 2016; Xavier, 2021; Coleman et al., 2021).

In terms of ancient life, one important concept is the last universal ancestor. For example, the last universal common ancestor is the ancestor of all presently living things (Weiss et al., 2016).

Four such last common ancestors are the above-mentioned last universal common ancestor (LUCA) and the last common ancestors of the three kingdoms of life - the last bacterial common ancestor (LBCA), the last archaeal common ancestor (LACA) and the last eukaryotic common ancestor (LECA). In this study, we use genes from gene repositories for LUCA (Weiss et al., 2016) and LBCA (Coleman et al., 2021).

The analyses of Betts et al. (2018) and Betts (2020) provide evidence that LUCA was a very ancient organism that existed close to the formation of the planet (> 4.5 Ga), with a predicted age between ~4 – 4.5 Ga. LBCA is estimated to have emerged from LUCA between ~3.5 – 4.0 Ga.

In this study, we see if there is evidence provided by phylogenetics that genes indispensable to present-day Gaia core attributes were also in LUCA and/or LBCA.

To do this, we seek sufficient genes to illustrate the existence of examples of each of the two core attributes of Gaia in LUCA or LBCA. At a minimum, sufficient modern genes also found in LUCA or LBCA would mean, for each of the two attributes, a minimum of one modern metabolic pathway and one gene from the full set of genes specifying the modern pathway.

This result would show that ingredients for Gaia were present early in life.

We also seek physical fossil morphology related to such genes from the era in which LBCA and/or LBCA emerged.

If these are found, we can argue that Gaia originated then, some 4 billion years ago.

It is not the aim of the present paper to resolve further questions, such as the specific steps that might have occurred over time since the origin of Gaia, to connect the earliest Gaias to modern global Gaia.

1.1. The Core Attributes of Gaia

To determine the core attributes of Gaia, we must first specify essential (necessary) attributes and separate them from other non-essential attributes. Kment (2021) describes a *necessary* truth as what must be the case and a *contingent* truth as what could be the case. Something necessary is part of the essence of an entity; something contingent is not.

An entity can have many attributes. To reduce this number, we introduce the concept of “core attributes”, the smallest number of attributes that distinguish the entity in question from all other entities.

To seek candidate attributes, we consider existing definitions of Gaia. In his book Expanding on Gaia, Lovelock (1978) wrote:

> *Margulis and I have since defined Gaia as a complex entity involving the earth's biosphere, atmosphere, oceans, and soil; the totality constituting a feedback or cybernetic system which seeks an optimal physical and chemical environment for life on this planet.*

A more recent description of Gaia from Lovelock (2003), cited favourably by Wilkinson (2015), is that:

> *… organisms and their material environment evolve as a single coupled system from which emerges the sustained self-regulation of climate and chemistry at a habitable state for whatever is the current biota.*

Looking at these definitions, the terms "feedback (system)", "cybernetic system", and "system from which emerges … self-regulation" are all equivalent attributes of a control system. A control system is defined (after Astrom and Murray, 2008) as a system that regulates the performance of another system. It does this by comparing the status of the performance variable being controlled with its desired value (or setpoint), and if there is a difference, applying a control action tending to bring the variable back to the same value as the setpoint.

Hence, the existence of a control system can be seen as one attribute of Gaia.

Two other attributes described are "planetary" and the involvement of "individuals in a group carrying out joint action".

To provide further information to assist us in determining which of these attributes of Gaia is necessary as opposed to contingent, let us now consider how these interpretations from the above definitions align with how Gaia is seen in the wider scholarly community. A search of scholarly publications for synonyms of the above terms is given in Table 1.

Table 1. Results for Gaia-related terms from searches of Google Scholar (accessed 24 March 2023)

Search term used	Number of results
Lovelock Gaia definition	20,500
Lovelock Gaia definition planet	15,600
Lovelock Gaia definition feedback	8,000
Lovelock Gaia definition homeostasis	4,770
Lovelock Gaia definition cooperation	8,190
Lovelock Gaia definition symbiosis	5,130

Table 1 shows the presence of the three attributes from the definitions, with the planetary attribute appearing most often. Despite this, it is proposed that the planetary nature of Gaia is nonetheless merely contingent. By way of analogy, taking an entity such as an aeroplane as an example, the existence of a large aeroplane does not preclude any smaller aeroplane being called an aeroplane. And so, with Gaia, we argue the planetary entity does not rule out the existence of smaller Gaias.

The remaining attributes are those of control systems in the individual organism and such individuals working jointly in a group.

Without the first attribute, there is no control capacity; without the second, there is no path to a massed effect. Hence, both of these can be considered necessary attributes.

These are, therefore, the attributes that will be used in this study and termed the “control system attribute” and the “joint action attribute”. The term “joint action” is used in preference to “cooperation” as we consider the selected term to be less teleological. As there are just two necessary attributes, these meet our definition of “core attributes”.

In seeking representative cases of the two proposed Gaia core attributes, we acknowledge at the outset that control systems must have originated very early in life’s history and for most or all of the cell’s metabolic processes; otherwise, the cell/protocell would have been unstable and fail to maintain structural integrity (Torday, 2015).

Further, the modern bacterium benefits from coordination between its individual intracellular metabolic processes (Kochanowski et al., 2021), and it is likely early prokaryotes would have also. If uncontrolled side-by-side metabolic processes in a cell or protocell had interfered with each other sufficiently, such entities would have ceased to function.

With this background, we note that this study does not purport to present*individual* empirical results or concepts that have not previously been reported. What we seek from the pool of such previously reported empirical results is a *set* of empirical results, that set not having previously been reported as a set, to provide evidence relating to a particular hypothesis.

1.2. Further aspects of the study

1.2.1. Time scales and stages of cellular aggregation

With the two core attributes of Gaia specified, the study seeks to identify the span of time over which each attribute can be observed, from the present to as far back in time as empirical evidence is available. This is sought across several scales of cellular aggregation – from unaggregated (single cells: bacteria) to grouped bacteria (biofilms), to multicellularity, and to large-scale multicellularity, including in vascular plants, particularly trees.

1.2.2. Types of Control System

In referring to control systems in the biological context (Billman, 2010), Walter Cannon in 1926 coined the term “homeostasis”. This term describes the regulatory process by which organisms maintain the constancy of their internal state in the face of their own changing needs in a fluctuating environment

Kotas (2015) has shown how biological homeostasis processes can be expressed in control system terminology.

Control systems are systems that carry out control actions to bring the performance of other systems back to a set point (Astrom and Edwards, 2008; Svrcek et al., 2014). The strength of a control action is termed its “gain”, and this can be proportional to the disturbance triggering it in various ways. It can be proportional to the disturbance linearly, to its integral or to its derivative. What is more, the overall output of a particular control system can involve combinations of these individual gains. Control systems, therefore, can be Proportional-only, Integral-only, Proportional-Integral, Proportional-Derivative and Proportional-Integral-Derivative (Derivative-only controls are not used in industry because derivative information only does not lead to useful control (Svrcek et al., 2014)).

The most common type of control system used in human industry is the Proportional-Integral-Derivative type. A Proportional-Integral-Derivative-Second-Order-Derivative control system is a further proposed elaboration on this type (Sahib, 2015; Raju et al., 2016). Empirical evidence was presented by Leggett and Ball (2021) that the planetary atmospheric control system is of the Proportional-Integral-Derivative-Second-Order-Derivative type.

1.2.3. On Gaia’s previously being typically thought of as a single planet-scale entity and an influential argument against Gaia relying on that idea

After Gaia was proposed, Dawkins (1982) defined Gaia as it was typically thought of at the time in terms of its planetary attribute. He used this definition as a premise that the standard neo-Darwinian unit of selection would, therefore, also need to be at planet level. Because neo-Darwinian evolution requires competition between multiple units of selection and there is only one biosphere, Dawkins claimed that Gaia could not exist given this situation because there were not multiple units of selection available for natural selection to work on.

This argument has been influential to such an extent that the matter, some 40 years later, has not been generally agreed upon as resolved, either theoretically or at the required empirical level. For example, Lenton et al. (2018) recently referred to the subject as an unresolved issue:

> *Most studies of Gaia presume that global-scale self-regulation involving life must arise through some form of natural selection, and then raise several problems, notably: selection amongst a population of interacting biospheres is not plausible…*

In this connection, Boyle and Lenton (2022) state:

> *Neither the biosphere as a whole, nor any planetary scale process or feedback, exhibits discrete replication*

> *analogous to that of organisms, or occurs in an interacting population of comparable entities. This has led many to the conclusion that any “Gaian” habitability-promoting influence cannot be the product of natural selection and is therefore either non-existent or somehow life-specific without being particularly Darwinian.*

It can be seen, then, that there has been a long impasse on this issue due to the assertion that Gaia cannot exist because it cannot have evolved by natural selection.

Recent conceptual advances have shown that Gaia can evolve by natural selection, albeit not by selection at gene level. This proposed mechanism involves persistence-based selection at the group (clade) level (Doolittle, 2014, 2019, 2020; Boyle and Lenton, 2022).

The aim of the present study (see Section 1 above) is to find sufficient genes for the two core attributes of Gaia in LUCA or LBCA for the purpose of showing that Gaia existed then. If that aim is met, the same evidence for those genes can also be used for the separate purpose of showing that planetary Gaia could have evolved from them in a standard gene-based Darwinian way. This would resolve the issue raised by Dawkins (1988).

1.3. Aim of the study

The aim of the study is to seek empirical evidence:

i. in an individual modern organism of at least one example of the Gaia core attribute of a control system; and
ii. in individual modern organisms, of at least one example of a group of organisms experiencing common joint action and carrying out such joint action that leads to beneficial results for the group; and
iii. for each of these attributes, of at least some of the modern genes and proteins central to their operation; and
iv. that these genes and proteins were also explicitly present in the earliest life (LUCA and/or LBCA).

2. Methods

This paper draws on studies from five areas:

1. morphology of the anatomical elements undergoing control and /or experiencing joint action;
2. in-vivo stimulus-response experiments, investigating the behaviour of individual anatomical components or organisms potentially experiencing control and/or joint action. Such experiments (Bailey, 2008) involve the investigation of time series of behavioural responses of organisms to applied stimuli (the treatment group) compared to time series of behaviour with no such stimulus applied (the control group).
3. genetics, looking for the genes specifying the anatomy and behaviour possibly undergoing control, including studies utilising gene mutations; and
4. phylogenetics, seeking evidence of any of the modern genes also being ancient, and
5. evidence from the physical fossil record that any of the modern morphology is also ancient.

Phylogenetics is the reconstruction of evolutionary lineages based on the study of inherited characteristics, particularly genes (Semple and Steel, 2003). The phylogenetics results used in this study are, in turn, derived from the field of phylogenomics already mentioned in the Introduction – the study of evolutionary relationships based on comparative analysis of the totality of the genes of an organism (that is, its genome) (Chan and Ragan, 2013). Phylogenomics involves the comparison of the genomes of many species using results from DNA sequencing. The more species to which a gene is common, the more ancient it is likely to be (Weiss et al., 2016).

Results from other methods, including from physical fossil evidence, are used to cross-check and add to the validity of these results.

With reference to the four-letter symbols used for genes and their corresponding proteins, italics and a lowercase initial letter are used in the symbol for the gene and plain (Roman) and an uppercase initial letter for the symbol for the protein (Stewart, 1995). For example, in bacteria, *cheY* is a chemotaxis gene; CheY is the corresponding protein synthesised from information in *cheY*.

The methodological process used in the study is hypothesis testing; the empirical information resource used is published literature.

3. Results

3.1. Gaia attributes and their genes

From the extensive literature on genes and their function, there are many cases that we consider related to Gaia attributes and their genes.

From these, we chose what we consider to be six representative examples. The cases are set out starting with planetary Gaia. The remaining cases commence with the simplest and progress to the most complex.

Case 1. Evidence for both core attributes: control system and joint action at the level of planetary Gaia

The empirical evidence for planetary Gaia and for a control system at that level was provided by analysis of time series using the method of Granger causality (Leggett and Ball, 2020). Leggett and Ball (2021) provided evidence that the control system was of the Proportional-Integral-Derivative-Second-Order-Derivative (PID2D) type.

Regarding the other core attribute of joint action at planetary level, we note that in Leggett and Ball (2021), we provided empirical evidence that the Normalised Difference Vegetation Index (a measure of the global aggregate of the photosynthetic activity of photosynthesising individuals) was the leading element of the control processes observed. These control processes were shown empirically to be subsequently applied to other physical elements of the atmosphere, such as wind and clouds. This is evidence that biological elements of the biosphere are applying a control system pattern to other elements of the atmosphere.

This interpretation is consistent with an interpretation in the IPCC Fourth Assessment Report by Denman et al. (2007), in which the pattern is seen as coming from the influence of the biosphere, particularly the land biosphere. They state (italics denote present author emphasis):

> *"Interannual and inter-decadal variability in the growth rate of atmospheric CO2 is dominated by the* ***response of the land biosphere to climate variations*** *… The terrestrial biosphere* ***interacts strongly with the climate****, providing both positive and negative feedbacks due to biogeophysical and biogeochemical processes … Surface climate is determined by the balance of fluxes, which can be changed by radiative (e.g. albedo) or non-radiative (e.g. water-cycle-related processes) terms. Both radiative and non-radiative terms* ***are controlled by details of vegetation.****"*

Both Leggett and Ball (2021) and Denman et al. (2007) lead to the interpretation that the signal seen at the global level must originate from individual organisms in the biosphere. For signals from individuals to add in such a way that there is a signal observable at the global level, not simply noise – this globally aggregated signal must (i) arise out of a dominant proportion of the individuals of the global biosphere and (ii) be sufficiently preserved to be seen in the globally aggregated output. This is explainable by a dominant proportion of the individuals of the global biosphere working in concert, a notion that matches the Gaia core attribute of joint action.

The scale of those involved in this joint action is striking: the land biosphere, just to take the dominant trees, consists of over three trillion individuals (Crowther, 2015).

Case 2. Control system core attribute: Single individual: unicellular prokaryote

In seeking the possible early emergence of a control system, we first specify a modern example in an individual organism.

The organism selected is the bacterium *Escherichia coli* (*E. coli*), and the example is the control of the behaviour of its flagellum.

The prokaryote flagellum provides motility (Bardy et al., 2003). It works like a propeller and is driven by what is essentially a motor – albeit biological and at the micrometre scale. Because, as a moving mechanical part, the flagellum can be observed in action, the modern prokaryote flagellum and flagellar movement have been extensively studied (for review, see Huang, 2019).

There is thus detailed knowledge of the structure of the flagellum, with significant work having also been done on the dynamics of flagellar operation and the nature of its control system (Alon et al., 1998; Yi et al., 2000). The method used by Alon et al. (1998) was a behavioural stimulus/response study of the dynamics of the flagellum during chemotactic motility. Since the initial bacterial chemotaxis study of Adler in the 1960s (Adler, 1966). *E. coli* has been the most prominent model organism used for chemotaxis studies. Over the following three decades, many biochemical and molecular studies have elucidated much about the molecular mechanism of chemotaxis operation in *E. coli* (for review, see Huang, 2019). In *E. coli*, the chemotaxis system consists of five transmembrane chemoreceptor proteins, Tar, Tsr, Tap, Trg, and Aer, and six core component proteins, CheA, CheW, CheY, CheB, CheZ, and CheR.

Of these proteins, CheY termed the chemotaxis response regulator, interacts with the flagellum and changes its direction of rotation.

The quantitative relationship between varying levels of CheY and bacterial swimming behaviour was investigated empirically by use of a computerised image analysis system (Alon et al., 1998). This system collected statistics on chemotactic responses by both free-swimming and individual tethered cells.

Alon et al. (1998) showed that despite stepwise increases in the level of external chemical stimulus, the level of CheY always returned to an initial setpoint.

Yi et al. (2000) showed that these results were consistent with control of the flagellum being of the Integral control system type.

With this established, we use phylogenomics to seek this Integral-type control system in as early life as possible. This requires a return to the nature of the structural and regulatory genes and proteins making up the bacterial flagellum.

In *E. coli*, the apparatus mediating bacterial chemotaxis comprises transmembrane receptors (methyl-accepting proteins) and the products of six *che* genes: *cheA*, *cheB*, *cheR*, *cheW*, *cheY*, and *cheZ.* Instead of *cheZ*, many chemotactic bacteria contain *cheC, cheD*, and/or *cheX* (Park, 2004).

Of these nine genes making up the chemotaxis apparatus, all but *CheY* are found in LBCA (see Table 2).

In terms of the Bayesian probabilistic method used by Coleman (2021), the eight genes found each displayed moderate to high probabilities of being present ($0.5 < PP < 0.95$) and therefore met the requirement of Coleman to have been a pathway likely to have been present in LBCA.

A separate line of evidence can be brought to bear supporting the early existence of *cheY*. Lai et al. (2020) note that the flagellar motor is currently the best-understood system for bacterial locomotion. There is evidence that the bacterial flagellar motor structure and amino acid sequence of constituent proteins are present across a diverse range of bacterial species and environments, suggesting an early origin (Lai et al., 2020).

Further, Lai et al. (2020) note that some species of the non-bacterial Archaea also possess flagella with rotary motors that drive swimming. While the structural proteins of the bacterial and archaeal motors differ, both motors use chemotaxis machinery that contains the protein CheY.

This suggests that *cheY* was present before the division of life into bacteria and archaea between ~3.5 – 4.0 Ga (Betts, 2020).

The Coleman (2021) and Lai (2020) results taken together give us evidence of the full set of chemotaxis genes in a modern bacterium also being present in LUCA or LBCA.

Alongside chemotaxis genes, in *E. coli*, about 50 genes have been found to be involved in either flagellar fabrication or non-chemotaxis operation (Lui, 2007b). Of these 50 genes, some 33 are found in LBCA (Coleman, 2021) (see Table 2), adding strong structural gene evidence to the chemotaxis gene evidence mentioned above.

The location of the integrator for the integral aspect of the control is a complex matter, not yet experimentally resolved (Araujo, 2022). For the purposes of this analysis, it is sufficient to note that the integrator must be either in one of the sets of proteins making up chemotaxis control or in their interaction as suggested by Alon (1998), who describes "…some hitherto undefined molecular interaction within the … network…"

From the foregoing, there are, therefore, multiple lines of evidence from phylogenetics placing the existence of genes for an Integral control system at the LUCA and/or LBCA stage of life.

Physical fossil evidence has been found for the early existence of the flagellum. Delarue et al. (2021) report the discovery in 3.4 Ga strata – dated by uranium-lead radiometric dating (Gardiner et al., 2019) – of unicellular microfossils exhibiting a tail-like structure. This tail-like appendage shares similar morphological features to locomotory organelles in modern microorganisms such as archaella, flagella, and cilia.

Considering the above genetic and physical fossil evidence overall, we can conclude that this provides empirical evidence for an entity (the flagellum) displaying a control system (of Integral type) in LUCA and LBCA near the start of life.

Case 3. Control system core attribute: Single individual: multicellular eukaryote

The organisms that are involved in modern planetary Gaia – in particular, the dominant organisms of the global biosphere (Leggett and Ball, 2021) – are predominately plants, mainly vascular plants and fungi. These occur within the kingdom of Eukarya. Some members of the Eukarya have flagella at some stages of their life cycle. However, these flagella involve a different mechanism and have no genes in common with those of the flagellum of bacteria or the Archaea (Jarrell and Albers, 2012).

If we wish to find a control system gene for homeostasis that is present in both LUCA and/or LBCA and also in organisms that are predominantly involved in modern Gaia (particularly, the vegetation of the global biosphere (Leggett and Ball, 2021)), we must identify a further candidate.

The tripeptide thiol molecule glutathione (GSH) is one such candidate molecule. Glutathione is present in all plants, animals, fungi, bacteria, and archaea (May et al., 1998; Pompella, 2003).

There is substantial evidence of the involvement of glutathione in cellular homeostasis. Pompella (2003) states that biomedical research has documented innumerable situations in which GSH participates in essential aspects of cellular homeostasis. In particular, GSH has a pivotal position in the process that regulates and maintains the balance between reducing and oxidising (redox) reactions in cells. This is termed cell redox homeostasis (Le Gal, 2021). The chemistry of life is based on such redox reactions (Williams et al., 1996; Falkowski et al., 2008).

The systems involved in keeping this cellular redox balance, including the glutathione system, have been extensively studied and characterised (Vergauwen, 2005). For example, in a stimulus-response study, Schafer (2001) showed that varying doses of glutathione made the redox level of the cell more stable than it otherwise would have been.

As mentioned previously, Kotas (2015) has shown how biological homeostasis processes can be expressed in control system terminology. He shows that integral control can be expected to be present in homeostasis of levels of cellular constituents. In the case of Schafer (2001), the levels of constituents being adjusted are oxidising and reducing factors, and the adjustment towards the specific redox setpoint is being carried out by glutathione. This is, therefore, expected to be done by integral control.

Modern glutathione is synthesised by a two-step process catalysed by two proteins, the enzymes γ-glutamylcysteine synthetase and glutathione synthetase. Genetically, γ-glutamylcysteine synthetase is encoded by the *gshA* gene, and glutathione synthetase is by the *gshB* gene (Wongsaroj, 2018).

Both genes have been found in ancient times: *gshA* in LBCA (Coleman, 2021) and *gshB* in LUCA (Weiss, 2016).

With these genes having been shown empirically to perform a specific role in creating homeostasis in modern life forms, their presence in LUCA or LBCA leads to the likelihood of the genes having performed the same role at that time.

This case, then, presents evidence that a gene for a control system involved in homeostasis in modern Eukaryotes, and in particular the vegetation of the global biosphere, was present from the start of life.

Case 4. Joint action core attribute: Joint action within an individual cell of multiple molecular pathways

The cases presented so far have considered the attribute of control systems at the level of the individual cell. This case considers individual cellular components within a single cell and seeks evidence for their joint action.

A central process in modern bacteria is breaking down (catabolising) carbon-based energy sources (such as glucose, lactose, or glycerol) available from their environment to generate energy for their life processes (Liu et al., 2020).

In line with this range of energy sources, bacteria possess a number of metabolic pathways; each pathway is tuned to catabolise a particular energy source. There can be a preferred energy source which is easiest to metabolise. This source is often glucose (Xiog et al., 2018).

When the preferred source is present, genes for the catabolism of less-preferred carbon sources are repressed (Liu et al., 2020). When the preferred carbon source is absent or is depleted, the genes for the catabolism of less-preferred carbon sources are activated (Singh et al., 2008).

This interplay of metabolic pathways to use different carbon sources at different times under specific environmental conditions allows organisms such as bacteria to maximise growth and survival (Singh et al., 2008; Reuß et al., 2018).

We consider that this coordination of the sequence of action of the above metabolic pathways to enhance benefit to the cell provides evidence for the joint action core attribute.

Turning to the other core attribute of the control system, we note that the example used in Case 2 (the flagellum) is a sub-cellular component.

Hence, the Case 2 example and this example together provide evidence of both the core attributes of Gaia being present within an LBCA cell.

Case 5. Joint action core attribute: Joint action between individual cells: unicellular prokaryote

Our evidence for joint action between individual cells is drawn from studies of a process in bacteria termed "quorum sensing". Wang et al. (2019) state:

> *The quorum-sensing (QS) system is an intercellular cell-cell communication mechanism that controls the expression of genes involved in a variety of bacterial cellular processes and that plays critical roles in the adaption and survival of bacteria in their environment. For intra- and interspecific communication, bacteria use chemical signals and their corresponding receptors. When an extracellular threshold concentration (analogous to a quorum) is reached, these molecules bind to their receptors, thereby activating the QS system.*

One of the main physiological processes controlled by quorum sensing is the formation of biofilms. Bacterial biofilms are surface-attached communities of bacterial cells embedded in an extracellular matrix composed of polymers produced by the microorganisms (Wang et al., 2019). They result from quorum sensing followed by coordinated action (biofilm formation), leading to net benefits for the bacterial community (for example, environmental stress reduction and resistance to antibiotics) (Flemming, 2016). Biofilms typically are made up of multiple species, including in the hundreds (Yang, 2011).

Quorum-sensing signalling molecules are termed autoinducers (AI). Four main general types of autoinducers have been described (Combarnous, 2020):

1. AI-1, mainly present in Gram-negative bacteria, are*N*-acylated homoserine-lactones (AHLs) with a core homoserine-lactone ring and a 4- to 18-carbon acyl chain with eventual modifications. The AHLs bind to specific LuxR-type cytoplasmic receptors, which control the transcription of numerous virulence genes, and to LuxN-type membrane receptors.
2. AI-2, present in both Gram-positive and Gram-negative bacteria, is considered to be a universal communication signal because LuxS, the key enzyme in AI-2 biosynthesis, is found to be widespread in both Gram-negative and Gram-positive bacteria (Xavier & Bassler, 2003).
3. AI-3, mainly in Gram-positive systems, typically uses secreted oligopeptides and two-component systems (TCSs), consisting of membrane-bound sensor kinase receptors (QseC) and cytoplasmic transcription factors (QseB) that direct alterations in gene expression.
4. PQS (pseudomonas quinolone signal) makes use of 2-heptyl-3-hydroxy-4(1H)-quinolone, which binds to its specific LysR-type transcriptional regulator receptor (PqsR) to control the synthesis of a rhamnolipid, which has a critical role in

the formation of the groupings of prokaryotes called biofilms.

Of the above four main types of autoinducers, the gene for only one is found in LUCA or LBCA. This is the *luxS* gene found in LBCA (Coleman, 2021), which produces Autoinducer-2 (AI-2).

That said, there is empirical evidence that AI-2 is an important autoinducer, playing, for example, a central role in biofilm formation and control.

For empirical evidence of this process, we refer to in-vivo stimulus-response experiments involving the effect of (AI-2 on biofilms (Li et al., 2015)

In the bacterium *Pseudomonas aeruginosa*, the addition of increasing amounts of exogenous AI-2 increased biofilm formation and bacterial viability. Yet higher concentrations of AI-2 reduced biofilm formation and bacterial viability. Gene expression analysis revealed that AI-2 increased the expression of quorum sensing-associated genes at lower concentrations and decreased these genes at higher concentrations. These results are homeostasis-like in that they control the outcomes –biofilm formation and bacterial viability – nearer to their optimal range than they otherwise would have been.

Similar results were found in the bacterium *Streptococcus suis* (Wang et al., 2019). The ability of *S. suis* to form biofilm was significantly increased when a small amount of AI-2 was added during growth. Further, deleting the *luxS* gene led to a decreased ability to form a biofilm.

Noting that the biofilm-inducing gene *luxS* is found in LBCA, we next seek physical fossil evidence for the existence of biofilms in the LBCA time period.

In the Strelley Pool Formation in Western Australia (dated to 3.46 Ga), Sugitani (2010) shows fossil evidence of features of microbial mats and stromatolites. Film-like microstructures have been recovered in this material (Delarue, 2020) and elsewhere (Westall et al., 2006; Sugitani et al., 2007, 2010). It has been proposed that the films possibly formed from fossilised extracellular polymeric substances (EPS) (Westall et al., 2006) secreted by prokaryotic microorganisms (Sugitani et al., 2010). EPS is the external structural element of a modern biofilm. Delarue (2020) notes that some film-like microstructures from the Strelley Pool Formation exhibit a striking morphological resemblance to modern EPS.

The film-like microstructures are made up of several morphological types. Taken together, the Sugitani and Delarue results suggest that biofilms made up of multiple species existed at the time of LBCA.

Hence, biofilms of that period would have benefited from a *luxS* process because of their capacity for coordination, including at the interspecies level.

In summary, this case shows:

- communication between modern individual unicellular organisms leading, in biofilms, to joint beneficial action and the involvement of the *luxS* gene;
- the essential gene for the modern process also being present in LBCA, showing that the same process could have

taken place in that time period; and
- corroboration from fossil evidence for the existence of biofilms in the LBCA era.

Case 6. Joint action core attribute: Joint action between individual multicellular organisms: woody plants (trees)

This case seeks to demonstrate joint action between individual woody plants – a prime constituent of modern planetary Gaia.

Here, we select a process that has been described for some time (Baldwin, 1983) in which an individual plant triggers mutually beneficial joint action in a group of surrounding individual plants. This most commonly occurs when a specific plant is in a group and is the first one to be stressed and/or damaged. The plant generates specific airborne emissions that are received by surrounding plants. If the surrounding plants are later stressed, they experience less damage because defences have been put in place as a result of the earlier receipt of the emissions.

Two main forms of stress on plants are stress on foliage from insect attack (herbivory stress) (Shiojiri, 2006) and metabolic stress from increased soil salinity (Caparrotta, 2018).

The following example involves the vascular woody plant, the conifer *Pinus sylvestris* (Scots pine), undergoing herbivory stress.

Pinus sylvestris occurs in the boreal forest that extends from Western Europe to Eastern Siberia, and the *Pinus* family is often dominant in this forest (Saucier, 2015). This forest comprises one-quarter of the global forest area (Crowther, 2015) and hence can be expected to play a major role in Gaia.

In an in-vivo stimulus-response experiment, *P. sylvestris* seedlings were exposed to either herbivore (weevil)-infested plants or undamaged plants (Yu, 2022). The results showed that herbivore-induced plant volatiles emitted by the weevil-infested plants decreased the amount of damage caused to plants that were later infested by weevils.

These results provide empirical evidence for both between-plant communication in conifers and on-off (switching) control.

Modern genes responsible for this process are now sought. This is complicated by the fact that Yu (2022) lists 51 separate volatile compounds as being emitted by the weevil-infested plants in the above experiments. It is not known how many of the 51 separate volatile compounds were responsible for the signalling.

What is known is that of these, a large majority – 47, or 84 per cent – are terpenes. Terpenes, and above all isoprene, induce stress tolerance in many types of plants (Sharkey et al., 2001; Vickers et al., 2009b; Velikova et al., 2011). The generality of the effects of isoprene in plants that have been studied has led to the suggestion of a general signalling function for isoprene in all plants (Harvey and Sharkey, 2016).

So, we can conclude that it is very likely that the terpenes emitted in the above experiments have a role in the response observed.

Despite there being so many terpenes involved in the P. sylvestris emissions, the specification of the modern genes for the terpenes is simplified. This is because all terpenoids originate from only two biochemical building blocks – isopentenyl diphosphate and dimethylallyl diphosphate (Hoshino, 2018).

Five genes associated with metabolic pathways involving one or both of these building blocks are reported in LBCA (Coleman, 2021):

The ***LldD*** gene: This generates type II isopentenyl diphosphate isomerase. This has the role of converting isopentenyl diphosphate from one physical form (isomer) to the form used as the terpenoid building block;

> *The **MiaA** gene: This generates dimethylallyl transferase. As for **LldD**, **MiaA** has the role of converting dimethylallyl diphosphate to the isomer used as the terpenoid building block;*
>
> *The **IspG** gene: The 2-C-methyl-D-erythritol 4-phosphate (MEP) pathway for isoprenoid biosynthesis is essential in most bacteria and plants (Campos et al., 2001). Campos et al. identified gcpE as a novel gene of the MEP pathway. The distribution of this gene in bacteria and plants strictly parallels that of the gene encoding 1-deoxy-D-xylulose 5-phosphate reductoisomerase, which catalyses the first committed step of the MEP pathway. Their data demonstrated that the gcpE gene is essential for the MEP pathway in **E. coli** and indicated that this gene is required for the trunk line of the isoprenoid biosynthetic route;*
>
> *The **IspH** gene: The **ispH** gene product has a role in a step of the non-mevalonate biosynthetic pathway leading to the universal terpenoid precursors, isopentenyl diphosphate and dimethylallyl diphosphate and*
>
> *The **XylB** gene: D-xylulokinase specified by the **xylB** gene catalyses the phosphorylation, converting unphosphorylated 1-deoxy-d-xylulose to terpenoids (Wungsintaweekul, 2001).*

The above shows that genes for the two biochemical building blocks for terpenes were present in LBCA. With terpenoids providing the means for joint action in the present day, it can be inferred that a similar process has been available since the time of LBCA.

3.2. Summary of Gaia attributes and genes common over time

Table 2 provides a listing from the preceding Case studies of the genes found in modem organisms that have also been found in LUCA and/or LBCA.

Table 2. Genes found in the Case studies in modern organisms that are also found in LUCA and/or LBCA.

Cases of Gaia core attribute/s and where found	**Key points**	**Modern genes also present in LUCA (Weiss et al. (2016) or LBCA (Coleman et al. (2021)**
Case 1: Control system and joint action core attributes: planetary Gaia	Control system evidenced by presence of PID2D signature in global temperature time series; joint action evidenced by fact that PID2D signature is observable time series aggregated at global level	Not applicable
Case 2: Control system core attribute: Single individual: unicellular prokaryote	Integral control of chemotaxis in *E. coli*	Eight chemotaxis (*che*) genes are found in LBCA: *cheA, cheB, cheC, cheD, cheR, cheW, cheX* and *cheZ*. *cheY* is reported for 3.4 Ga by Lai et al. (2020). 33 flagellum-related genes are found in LBCA: *fapA, flaG, flgB, flgC, flgD, flgE, flgG, flgH, flgJ1, flgK, flgL, flgM, flhA, flhB, flhG, fliD, fliF, fliG, fliH, fliI, fliJ, fliK, fliL, fliM, fliN, fliP, fliQ, fliR,, fliS, hrcA, motA, motB,* and *swrD*
Case 3: Control system core attribute: Single individual: multicellular eukaryote	Unicellular and multicellular, single molecular pathway; glutathione metabolism	Two genes: *gsbA* in LBCA; *gsbB* in LUCA
Case 4: Joint action core attribute: Joint action inside an individual cell of multiple molecular pathways	Coordination of multiple molecular pathways for metabolism of multiple energy sources	Three genes in LBCA: *disA, cyaA* and *lacD*
Case 5: Joint action core attribute: Between individual cells - unicellular prokaryote	Communication and coordination between multiple unicellular individuals; bacterium *Pseudomonas aeruginosa*	Three genes in LBCA: *luxS, med,* and *rbsB*
Case 6: Joint action core attribute: Joint action between individual multicellular organisms: woody plants (trees)	Communication and coordination between multiple multicellular individuals; forest tree *Pinus sylvestris*	Two terpenoid precursor genes in LBCA: *lldD* and *miaA*

From Table 2, it can be seen that the forgoing case examples involved a total of 56 modern genes for the core attributes of Gaia being shown also to exist in LUCA or LBCA – 43 for the control system core attribute of Gaia and 13 for the core attribute of the joint action of individuals.

4. Discussion

The present study began by exploring the question of what might comprise the necessary attributes of Gaia. We made the case that planetary Gaia was one type of Gaia, but the planetary aspect was a contingent rather than a necessary attribute. We proposed two core attributes for Gaia – the presence of control systems in each individual and groups of such individuals carrying out joint action to produce results more beneficial to the group than would have come about from each individual acting in isolation.

We then sought representative examples of each of the core attributes of Gaia in operation in present-day life. Representative genes necessary to the genetic specification of each example were identified. These same genes were then sought in the earliest examples of life that have been genetically characterised in empirical terms – the Last Universal

Common Ancestor (LUCA) and/or the Last Bacterial Common Ancestor (LBCA).

Using this approach, we have presented empirical evidence for the existence of separate specific genes contributing to the functioning of examples of each of the two proposed core attributes of Gaia near the start of life (in LUCA and/or LBCA) and the same genes carrying out the same role for the same core attributes today.

The range of physical scales where these results were found started from below the level of the single cell, with both Gaia core attributes being found there. The control system core attribute is found to operate on an individual prokaryotic intracellular process (flagellar control). The core attribute of joint action is shown to involve several individual intracellular processes.

At the next scale-up involving the individual cell, the relevant evidence was of the flagellum providing chemotaxis functionality to the prokaryote cell.

In particular, the LBCA cell displays genes for both Gaia core attributes: control systems (control of flagellar function) and joint action (in the processes of biofilm construction).

The notion of joint action next has meaning at the level of interaction between individual cells. Here, we saw the core attribute of joint action of many individuals and, further, the core attribute of control systems present and coordinating such joint action.

Finally, in the most recent multicellular stage of life, we provided examples of both core attributes of Gaia in action – the presence of control systems and joint action between multicellular organisms to achieve better outcomes for the group.

Dawkins (1982), defining Gaia in terms of its planetary attribute, which posits that there is *one* Gaia on Earth, pointed out that neo-Darwinian natural selection requires competition between *multiple* units of selection. Given the absence of such multiple units of selection, Dawkins claimed that Gaia could not come into being by neo-Darwinian natural selection and, therefore, did not exist.

Specifically, Dawkins wrote (Dawkins, 1982, page 358), applying gene-centred evolution - that is, with the gene as the unit of selection - to Gaia:

Homeostatic adaptations in individual bodies evolve because individuals with improved homeostatic apparatus pass on their genes more effectively than individuals with inferior homeostatic apparatuses. For the analogy to apply strictly, there would have to have been a set of rival Gaias, presumably on different planets.

With regard to this claim, the present study has now provided evidence that Gaia can exist at a range of scales below planet level and that genes for the core attributes of Gaia have been available at these lower scales from near the start of life (in LUCA and/or LBCA). With respect to the chronological time period in which ancestral life such as LUCA might have appeared, Betts et al. (2018) date the emergence of LUCA to not later than 3.9 Ga.

With such genes being a unit of selection, planetary Gaia can come about by a series of developments commencing near the start of life, and each involving standard – that is, gene-based – Darwinian natural selection.

We consider these results to resolve the issue raised by Dawkins (1982).

5. Concluding remark

The two proposed core attributes of Gaia, having been shown to be in operation at the first cellular stage of life, means that at this first stage, the cell had a degree of control over both its interior components and its response to its external environment.

Further, because controls would have operated on many (if not most) of the cell's processes, and they would have to have operated with at least adequate coordination, the first successful cell can be seen as a Gaia itself.

So, from at least as early as LUCA to the present, every combination of living cells – first into biofilms and later into multicellular organisms – has been a combination of Gaias.

This joint action of life forms is next seen to combine right up to the level of involvement of the whole biosphere, finally giving us the Gaia concept as first presented to science by Lovelock some fifty years ago – planetary Gaia.

Data Availability

All data underlying the study are available from the references cited.

Appendix 1

In Greek mythology, the goddess Gaia is the personification of the Earth, and one of the Greek primordial deities (Theodossiou et al., 2011). The use of a deity's name to name the Gaia hypothesis (Lovelock, 1972) has drawn criticism (for example, Postgate, 1988; Martin, 2005).

We therefore note that in other cases, biological terminology has also been based on names of deities and has been accepted. Examples include the Archean phylum Asgardia (Zaremba-Niedzwiedzka et al., 2017; Wu, 2022) (in Nordic mythology, Asgard is a location associated with the gods (Lindow, 2002)); and the boreal forests (from *Boreas*, the Greek god of the cold north wind, storms and winter) (Luoranen et al., 2023).

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