Hominid evolution: genetics versus memetics.

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Abstract.

The last few million years on planet Earth have witnessed two remarkable phases of hominid development, starting with a phase of biological evolution characterised by rather rapid increase of the size of the brain. This has been followed by a phase of even more rapid technological evolution and concomitant expansion of the size of the population, that began when our own particular "sapiens" species emerged, just a few hundred thousand years ago. The present investigation exploits the analogy between the neo-Darwinian genetic evolution mechanism governing the first phase, and the memetic evolution mechanism governing the second phase. From the outset of the latter until very recently – about the year 2000 – the growth of the global population N was roughly governed by an equation of the form $\dot{N} = N^2/\tau_\star$, in which $\tau_\star$ is a coefficient introduced (in 1960) by von Foerster, who evaluated it empirically as about 2×10^{11} years. It is shown here how the value of this hitherto mysterious timescale governing the memetic phase is explicable in terms of what happenned in the preceding genetic phase. The outcome is that the order of magnitude of the Foerster timescale can be accounted for as the product, $\tau_\star \approx \tau_g\, I$, of the relevant (human) generation timescale, $\tau_g \simeq 20$ years, with the number of bits of information in the genome, $I \approx 10^{10}$.

Keywords: hominid, homo sapiens, evolution, meme, gene, genome.

1. Introduction

The global "high tech" civilisation now dominating this planet is the culmination of a few million years of hominid evolution that can be described in terms of two main phases. The first began when our ancestral line branched off from that of the chimpanzees, at what may have been the last evolutionary hard-step [1, 2, 3]. This step is the latest of the 39 bifurcations[4] listed by Dawkins (whose introductory presentation of the anthropic principle did not address the terrestrial hard-step question, but got sidetracked into far fetched cosmological speculations).

On the basis of the meagre palaeontological evidence available, the salient feature of the first phase was systematic growth of cranial (and presumably corresponding intellectual) capacity, which proceeded at a modest rate in the genus australopithecus, and became remarkably rapid after our own genus homo had branched off – at what is an alternative candidate for hard-step status – a couple of million years ago.

The second phase started relatively recently when our own particular species, homo "sapiens" finally emerged, just a few hundred thousand years ago. Instead of the genetic evolution that characterised the previous phase, this second phase – which has lasted until now – has been characterised by technological evolution and concomitant population expansion to fill the increasing range of newly created ecological niches. Such evolution is describable as memetic, because the technological know-how on which it depends is analysable in terms of memes, meaning replicable cultural information units, a fruitful concept originally introduced by Dawkins, who drew attention [5] to the analogy between memetic evolution and ordinary genetic evolution as described by neo-Darwinian theory.

The purpose of the present article is to point out some interesting quantitative consequences that can be obtained by taking this analogy seriously, on the basis of the presumption that the relevant selection pressure – favouring increasing mental capability during the first phase, and increasing technological capability during the second phase – would have been sufficiently high to determine the direction of progress, of which the actual rate would however have been controlled just by the size N of the relevant interbreeding population (in the manner described by the simplified model of neo-Darwinian evolution [1] recapitulated in the Appendix).

2. Rudimentary esssentials of neo-Darwinian theory

Although satisfactory for the description of large bodies, classical physics as developed before the twentieth century was inadequate for the description of smaller systems, which need allowance for atomic substructure and the use of quantum mechanics. In an analogous way, classical Darwinian theory – treating evolution as a continuous process – is adequate only for very large populations. A less naively simple description is needed for small and medium sized populations, meaning those in which

$$N \lesssim N_r \,, \tag{1}$$

where N_r is the replication reliability number, meaning the number of successive generations over which one would expect the genetic information at a particular locus to be reliably copiable without mutation under favorable conditions.

The discrete nature of genetic information, was first pointed out by Mendel in Darwin's time, but it was was not until after Morgan's observational discovery of the mutation process that the neo-Darwinian theory needed to allow for the finiteness of the mutation rate was was developed [6] by pioneers such as Wright and later on Kimura. Although very small, the rate $r \approx 1/N_r$ of mutations at a given genetic site must be non-zero in order for long term evolution to be possible. The total number of mutations per generation will have order of magnitude given by $\mu \approx Ir$, where I is the number of bits of information in the genome, which is identifiable (modulo a factor of 2 to allow for the use of a four letter coding) with the number of sites, so we shall have $N_r \approx I/\mu$.

As most mutations will be harmful and many fatal, it is necessary for individual survival the μ should not be too large compared with unity, while a value that was unnecessarily small would be bad for the flexibility needed for long term evolutionary adaptability. It is therfore to be expected – and is confirmed [6] by observation – that long term evolution would have adjusted the mutation rate to be of the order of unity, so one obtains

$$\mu \approx 1 \;\Rightarrow\; N_r \approx I \,, \tag{2}$$

with the actual value of this genome information content I given in order of magnitude (for the eukaryotic cells of multicellular organisms such as ourselves) by $I \approx 10^{10}$.

In order for favourable mutations at many different sites to be selectable simultaneously it is important that genetic information should be efficiently exchanged throughout the population concerned. The analogous process for memes has been largely dependent on language, and has been greatly accelerated by the invention of the printing press and most recently the internet. In the genetic case, the correponding process is of course achieved by sex, which involves many complicated details (starting with the distinctions between male, female, and sometimes hermaphrodite, genders). As detailed treatments allowing for such intricacies tend to be rather elaborate [6], I have formulated a cruder simplified description [1] that is recapitulated in the appendix, which should, I trust, be adequate for our present purpose. It is to be emphasised that classical Darwinian theory is not adequate for this purpose, because our concern here is with hominids, for whom the global population N (and hence *a fortiori* the population of all effectively interbreeding subunits) has always been below the limit (1). The coincidence that we are getting near this classical limit right now will be seen to be of portentous significance.

The simplified description in the Appendix is based just on the two dominant variables, which are the ordinary Darwinian selection coefficient s for the variant in question, and the breeding population number N. The third relevant parameter, N_r, is not (or hardly) a variable, but has a roughly fixed value with order of magnitude given [6] in accordance with (2) by

$$\sqrt{N_r} \approx 10^5 \,. \tag{3}$$

As shown by Figure 4, this value determines the classification of the 2-dimensional (s versus N) parameter space into four zones labelled A,B,C, D, of which the last is that of classical Darwinian evolution at a rate proportional to s, while A and B are those for which s is too small to avoid being overwhelmed, either by random fluctuation which dominate in A, or by random mutations, which dominate in B.

The zone that is most relevant for our present purpose is the one labelled C, which is defined by the condition that the selection coefficient be large enough to determine a consistent direction of evolution, but unable to determine the rate of evolution, which will be limited by shortage of mutations in the small and moderate populations characterised by (1). In this case it follows that the relevant evolution timescale τ will be given as a multiple of

the generation timescale τ_g by the prescription

$$\tau \approx \tau_g \, N_r/N \,, \tag{4}$$

 This formula specifies the minimum timescale required for veritable genetic evolution in a population with the given value of N in the range (1).

That minimum value (4) will be actually obtained for quite moderate values of the Darwinian selection coefficient s for a population not too far from the critical value $N \approx \sqrt{N_r}$, as given by (3), a condition that would indeed seem to have been satisfied by the hominid population in the first phase, prior to the proliferation of homo "sapiens". The population in those days would have consisted of small scattered clans or tribal groups of which the (climate dependent) total would have fluctuated widely, with a typical value given perhaps by $N \approx 10^5$ and a maximum that would probably not have exceeded about a million. If we assume that the generation timescale would have been $\tau_g \simeq 25$ years, and that the maximum population was $N \approx 10^6$, then it follows from (3) and (4) that the minimum timescale needed for substantial evolutionary change would have had order of magnitude

$$\tau \approx 250 \text{ thousand years} \,, \tag{5}$$

 while the typical requirement would have been more like a million years. As these values seem to agree with the timescales indicated by the fossil record – particularly of cranial expansion – it would appear that the selection pressure must indeed have been high enough to keep this hominid evolution process going at the maximum genetically allowable speed.

3. The memetic analogy

The genetic evolution timescale given by the formula (4) is inversely proportional to the population N because the rate of occurence mutations (at any particular site) will be proportional to the total population concerned. In the analogous case of memes, one would expect that the rate of occurrence of ideas (of any particular innovative kind) would also be proportional to the size of the population concerned, and hence that the coorresponding memetic timescale τ would similarly be inversely proportional to the relenant population size N. This means that it will be given by an expression of the form

$$\tau \approx \tau_\star/N \tag{6}$$

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in which the coefficient $\tau_\star$ is a timescale that will presumably depend on the qualitative nature of the people concerned, particularly the cleverness of the fraction that is brightest

Early in the first phase of the hominid evolution process, three or four million years ago, the archaeological evidence indicates that, as one would have expected, the rate of technical progress was low, with a timescale long compared with the value given by (5). This evidently means that the coefficient $\tau_\star$ in (6) would have been long compared with the product,

$$\tau_g \, N_r \approx 250 \text{ thousand million years}, \tag{7}$$

in (4). However as their brains got larger and the hominids became cleverer, the capabilities of their technological innovators would have increased, and so the value of the coefficient $\tau_\star$ would have decreased until it reached a critical value given by

$$\tau_\star \approx \tau_g \, N_r \,, \tag{8}$$

beyond which the rate of technical progress would have become more rapid than biological evolution.

It would appear that this is indeed just what happened – in other words genetic evolution was overtaken by memetic evolution – at the transition to the second phase of hominid evolution, when modern homo "sapiens" emerged, just a few hundred thousand years ago.

4. The onset of population expansion

The question of whether natural selection acts primarily at the level of individuals or rather at the level of groups has been debated since Darwin's time. It has been suggested that the issue might be transcended by reformulating the problem from the point of view of genes [5] rather than complete organisms, but that rather begs the question, as it is still necessary to worry about whether it is a matter of individual genes or groups of genes. Whichever formulation is preferred, it is now generally recognised [7] that the relative dominance of individual or group levels will depend on cirumstances.

In palaeolithic times, before the development of agriculture, competition seems to have operated particularly strongly at the level of small clans or tribal groups. For such a group, one of the main advantages of relative progress, whether genetic, in the form of bigger brains, or memetic, in the form of better technology, would simply have been that it reduced the risk of succumbing to genocide, a common ultimate fate of clans whose development

lagged behind. The failure of most such groups to leave a significant number of descendents is evidenced [8] by the discovery that the "effective" ancestral population size obtained from analysis of the modern human genome is only of the order of a few tens of thousands – the equivalent of a single middle sized tribe – whereas the global population would at most times have been much larger than that.

As well as being essential for survival in the inter-group competition for occupancy of the preexisting ecological niches of the hominids, another advantage of progress – particularly the memetic kind exemplified by the use of fire – would have been to expand the range of accessible niches and thereby increase the global population N. This population expansion mechanism seems to have already started to operate, albeit modestly, in the first hominid phase (before the emergence of homo "sapiens") when homo "erectus" came out of Africa [9, 10] to colonise many parts of Asia. Since the second (memetic) phase got under way, successive frequently overlapping waves of technologically empowered population expansion have been of paramount importance, a salient early example being that of the "exodus", when homo "sapiens" sallied from the warmth of Africa to confront the Neanderthals in cooler Europe, as well as the more ancient "erectus" population in Asia, at about the time [8] when the habitable climate range was greatly expanded by the development of cloths.

5. The memetic growth law

The rate of change $\dot{N}$ of the population size N is characterisable at any instant by a corresponding growth timescale defined by setting

$$\dot{N}/N = \tau. \tag{9}$$

During the memetic phase, when the growth is primarily attributable to technical progress of one kind or another, this time scale can be expected to be roughly given by the corresponding memetic timescale τ that is given in terms of the loosely defined memetic coefficient $\tau_\star$ by the formula (6).

The implication is that to describe the memetic phase one should combine (6) and (9), thus defining this coefficient more precisely by setting

$$\dot{N}/N = N/\tau_\star. \tag{10}$$

If we now suppose, as a plausible and testable hypothesis, that this coefficient $\tau_\star$ is insensitive to conceivably relevant details of social organisation, but
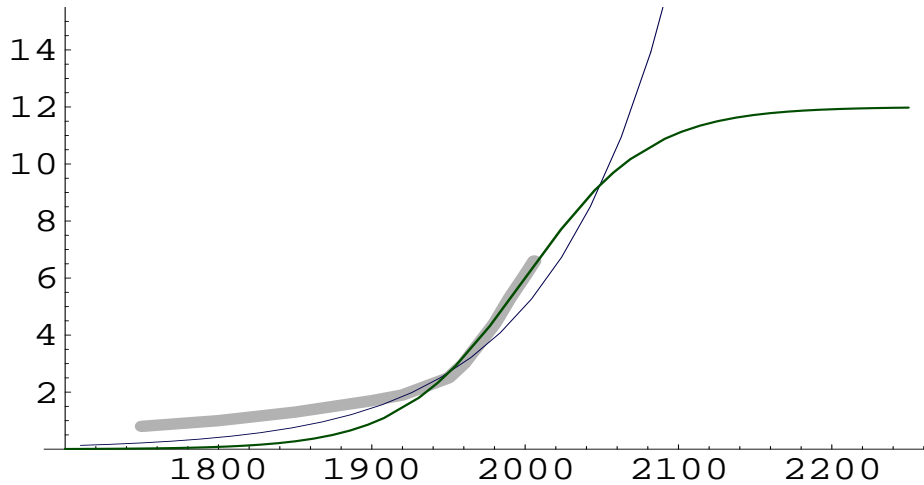
Figure 1: Plot of global population N, in units of 10^9, against date, using thick pale shaded curve for U.N. statistics from 1750 A.D. to 2000 A.D. The thin dark curve shows crude Malthusian matching of the exponential formula (11) to what was observed in 1950 A.D. by taking $\tau \simeq 80$ yr, which overestimates future but underestimates present and past. The firm pale curve shows "orthodox" Verhults type matching using the logistic formula (13) fitted to the latest observations, with inflection about 2000 A.D., by taking $\tau \simeq 40$ yr. This again underestimates earlier values, while overestimating what is plausible in the long run, as its measure $\mathcal{A}$ (proportional to the area under the curve) will diverge linearly.

depends only on the innate intelligence distribution of the population in question, it follows that it will not have had time to change substantially since our species first emerged. Indeed the reason why we consider ourselves to be of the same "sapiens" species as our ancestors more than a hundred thousand years ago is that our palaeontologically detectable morphological development since then has been relatively insignificant. On the basis of the postulate that, since that time, the coefficient $\tau_\star$ has been approximately constant, with the value given roughly by the critical transition magnitude (8), the memetic growth law (10) acquires the status of a verifiable prediction.

In the remainder of this article it will be shown that the available historical and archaeological evidence confirms that the substitution in (10) of the fixed value given by (8) provides a demographic model – of hyperbolic type –that does indeed work remarkably well.

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6. The ill fitting exponential, Verhults, and Huppert type models

Before proceding, it is to be recalled that the theory of demographic growth has a history dating back to the work of Malthus, who introduced the simplest and still most widely used kind of model for this purpose, namely that of the exponential type obtained by taking the timescale τ in (9) to have a fixed value, in terms of which the solution will take the form

$$N = N_0 \exp\{t/\tau\}, \tag{11}$$

where N_0 is the population at some chosen time origin when $t = 0$.

Although the recipe for perpetual exponential growth is still commonly sought as an ideal "holy grail" by economists, its ecological impossibility in the long run was clearly recognised by Malthus himself. The first and simplest "sigmoid" model allowing for the limited availability of renewable resources was introduced by his follower, Verhults, in the middle of the nineteenth century, but it took another century before attention began to be given to the need to take analogous account of the limited availability of non-renewable resources, for which a corresponding "peaked" model was introduced by Huppert.

The simple ecological model due to Verhults is based on an evolution equation of what is known as the logistic form,

$$\dot{N}/N = (1 - N/N_\infty)/\tau, \tag{12}$$

for some fixed saturation value N_∞, interpretable as the maximum environmentally sustainable value of N. (For example, if one allows about an acre for a family of four, the entire land surface of the world gives $N_\infty \approx 10^{11}$.) The solution of the Verhults equation (12) will be be symmetric with respect to a time t_s in terms of which it takes the well known logistic form

$$N = \frac{N_\infty}{2}\left(1 + \tanh\left\{\frac{t - t_s}{2\tau}\right\}\right), \tag{13}$$

which shows how the upper bound N_∞ will be asymptotically approached from below. The smoothly controlled Verhults model was originally intended for application, not to the world as a whole, but just to the newly established kingdom of Belgium, for which it was remarkably successful. However – as an example of the more unpleasant alternatives about which Malthus had warned – in Ireland about the same time, exponential growth was terminated,

not by smooth convergence to a plateau level, but catastrophically by a famine.

As the twentieth century advanced, people began to worry about a limitation of a different kind. As well as the problem of saturation of renewable resources, there is the problem of exhaustion of non-renewable resources. In order to treat such problems, it is useful to think not so much in terms of the instantaneous population size N but rather in terms of its time integral $\mathcal{A}$ say. Starting from any chosen time origin, this measure is defined by the condition that its time derivative be given by

$$\dot{\mathcal{A}} = N \,. \tag{14}$$

which means that $\mathcal{A}$ will be proportional to the corresponding area under a curve of the kind shown in Figure 1. If the rate of consumption of some non-renewable resource is proportional to the number of people using it, then $\mathcal{A}$ will measure the extent to which that resource has been used at the time under consideration.

As for the exponential model (11), this quantity – which I shall refer to as the anthropic measure – will grow without bound, $\mathcal{A} \to \infty$ as $t \to \infty$, even for a Verhults model, for which it will be given by the formula

$$\mathcal{A} = N_\infty \tau \ln\left[1 + \exp\left\{\frac{t - t_s}{\tau}\right\}\right] \,, \tag{15}$$

so that, as can be seen from Figure 1 its time dependence will ultimately be linearly divergent.

To take more realistic account of the finitude of non-renewable ressources the most commonly discussed models are of the kind introduced in the context of oil extraction by Huppert (a Shell engineer) who recognised that models of the logistic kind described above are plausibly applicable to accumulated consumption of a non-renewable ressource such as oil. If maintenance of an acceptably high standard of living requires a proportionate rate of consumption of such ressources, the implication is that the logistic model would be applicable not to the instantaneous population N as supposed by Verhults, but to the accumulated anthropic measure $\mathcal{A}$ defined by (14), whose evolution would therefor be governed by an equation of the analogous form

$$\dot{\mathcal{A}}/\mathcal{A} = (1 - \mathcal{A}/\mathcal{A}_\infty)/\tau \,, \tag{16}$$

for some constant $\mathcal{A}_\infty$ that is interpretable as the total anthropic measure of the entire past and future.
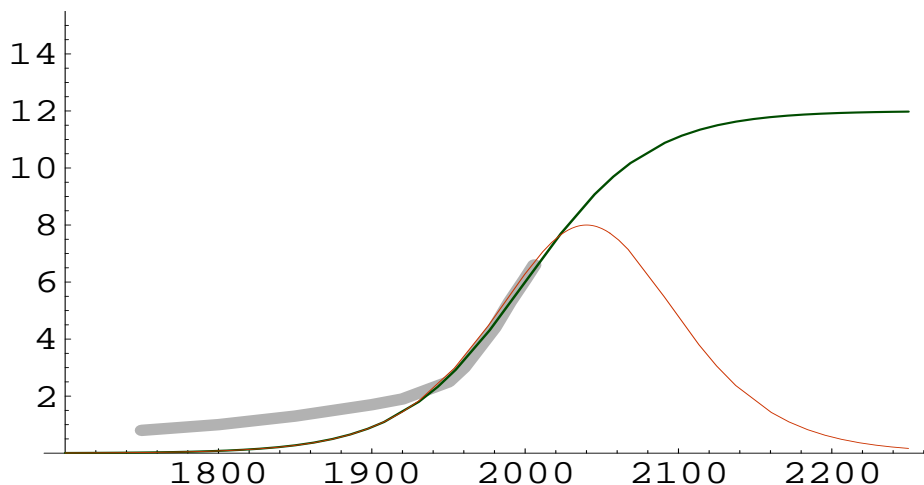
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Figure 2: As for Figure 1 with medium thickness curve showing "orthodox" matching by a Verhults model, but with the crude exponential model replaced by a Huppert type logistic derivative model (18) fitted as shown by thin pale shaded curve to the latest observations, about 2000 A.D., by taking peak time t_p about 2040 A.D., and setting the peak population to be $N_p \simeq 8 \times 10^9$, again with $\tau \simeq 40$ yr. Although finiteness of area under this curve allows convergence of anthropic measure – to the limit $\mathcal{A}_\infty = 4\tau N_p \simeq 10^{12}$ human years – this peaked matching still underestimates values at earlier times.

As the analogue of (13) the solution of this equation (16) will have the logistic form

$$\mathcal{A} = \frac{\mathcal{A}_\infty}{2} \left(1 + \tanh \left\{ \frac{t - t_p}{2\tau} \right\} \right) , \qquad (17)$$

in which t_p is a constant of integration that is interpretable as the time at which the corresponding total population

$$N = \mathcal{A}_\infty / 4\tau \cosh^2 \left\{ \frac{t - t_p}{2\tau} \right\} , \qquad (18)$$

reaches its peak value, namely $N_p = \mathcal{A}_\infty / 4\tau$. Although this kind of model may be useful for the description of what may happen in the short term future, it is clear from Figure 2 that it fails as badly as the simple exponetial model and the Verhults model for the description of global demography in the distant and even recent past.

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7. The well fitting Foerster model

It was reasonable for economists and social scientists such as Verhults, and other early followers of Malthus, to seek timescales of the order of a human lifetime, or at most of the duration of human history, for the formulation of their demographic models. When simple models involving a single such timescale τ were found to be inadequate, they resorted [11] to elaborate multi-timescale models with too many adjustable parameters to be of much help for prediction. It was hard to see that the available demographic data were after all describable very well in terms just of a single timescale, $\tau_\star$, because the required value is literally astronomical. It is therefor unsurprising that the first to have recognised it should have been not an economist, or even an ecologist, but a physicist, Heinz von Foerster (1911-2002) from Vienna, who noticed at last[12] that the available demographic data could be fitted rather well by a formula of the simple hyperbolic form

$$N = \frac{\tau_\star}{t_d - t} \,, \tag{19}$$

which is exactly what is obtained from the memetic evolution law (10) derived above, subject to the specification of a divergence time t_d that arises as a constant of integration.

The validity of this formula – as a fairly good approximation with a roughly constant value of $\tau_\star$ all the way from palaeolithic to modern times – did not become widely known until relatively recently, and is something I observed independently, before finding out that it had already been pointed out in 1975 by von Hoerner [13], and back in 1960 by von Foerster [12], who estimated that the remaining time before the singularity was then barely 70 years. More than half that time has since been used up, but the remarkable – and rather alarming – fact is that significant deviation from the Foerster formula has not yet become clearly observable.

Theoretical explanations of the acceleration from an initially slow start (what has been referred to by Renfrew as the "sapient paradox" [14]) and more particularly of the quadratic form, $\dot{N} \propto N^2$ of the relevant growth law (10), have been proposed by Kremer [15] and Koratayev [16] in terms of theories of technological development along lines similar to those sketched in Section 4, but without reference to the neo-Darwinian genetic evolution process in the pre-memetic phase of hominid evolution that determines the actual value of the required coefficient $\tau_\star$. The rough estimate obtained for
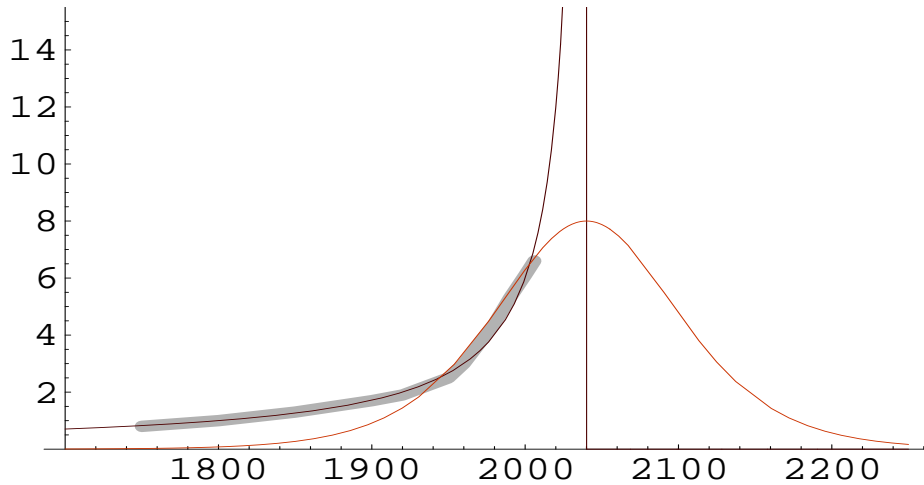
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Figure 3: As for Figure 2 but (instead of "orthodox" matching) using thin dark curve to show successful matching of past population, up to the date $t_2 \simeq 2000$ A.D., by a Foerster model, as given by (19) for $\tau_\star \simeq 24 \times 10^{10}$ yr, with divergence date $t_d \simeq 2040$. Unlike the Huppert model plotted by a thin pale curve as before, this simple hyperbolic model is realistic as a description of the past, but in view of its divergence at the "doomsday" date t_d (when the Huppert model passes through its peak) its hundred thousand years of approximate validity must come to an end wihin a few years from now.

this by substituting (7) in (8) agrees very well with the more precise value

$$\tau_\star \simeq 240 \text{ Gyr} . \tag{20}$$

that I obtain, as shown Figure 3, by matching the formula (19) to the official U.N. statistics [17] up to about 2000 A.D., with the correspondingly adjusted value of the constant of integration – namely the divergence date – given by

$$t_d \simeq 2040 \text{ A.D.} \tag{21}$$

It is to be remarked that, on the basis of fine tuning to the demographic statistics of their own time in the short run, von Foerster [12] and von Hoerner [13] originally suggested a "doomsday" time that was even nearer, $t_d \simeq 2025$ A.D., in conjunction with a fixed timescale that was correspondingly reduced, $\tau_\star \simeq 200$ Gyr. However the rather longer fixed time scale (20) and the rather

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later divergence time (21) seem to give a better match in the long run, not just for more recent years, but also for the more distant past, through mediaeval times. For even earlier (classical, bronze age, neolithic, and palaeolithic) times [11] the uncertainties are anyway so large that the differences between such alternative adjustments are not statistically significant.

According to (19) and (20) the size of the global population at the time, t_1 say, of the begnning of the memetic phase, a few hundred thousand years ago, would have been given roughly by $N_1 \approx 10^6$ an order of magnitude that is consistent with the estimates discussed in Section 3. Much of that total would not have been direcly ancestral to ourselves, but would have included various "erectus" and Neanderthal populations, as well as many "sapiens" groups that subsequently died out without leaving any descendants. In terms of this initial value N_1 the subsequent measure, attributable almost entirely to our own species, will be expressible as

$$\mathcal{A} = \tau_\star \ln\{N/N_1\} \,. \tag{22}$$

Up to the present time the expansion factor N/N_1 is about $10^4 \simeq \mathrm{e}^{10}$, so it follows from (20)and (22) that the measure of the whole of our "sapiens" species until now is given roughly by $\mathcal{A} \approx 2.4 \times 10^{12}$ human years.

8. Conclusions

It is remarkable that the formulae (19) and (22) are still valid as reasonably good approximations even today, but it is evident that this can not go on for much longer. It is not reasonably conceivable that the hyperbolic Foerster model should remain valid beyond a crescendo point that will be attained when the remaining time before the "doomsday date" t_d has become short compared with the reproductive breeding timescale τ_g, so that population expansion will be unable to keep up with the possibilities provided by technical progress, even if the latter continues. According to (8) and (19) this will occur when the population approaches the maximum allowed by (1), with magnitude $N \approx I$.

It is clear that we shall have reached this crescendo point within at most a few years from now. What will happen after that? Most of those alive today can expect to live long enough to find out. The results of the present work are pertinent for addressing this question within the framework of the anthropic principle [1, 18, 19].
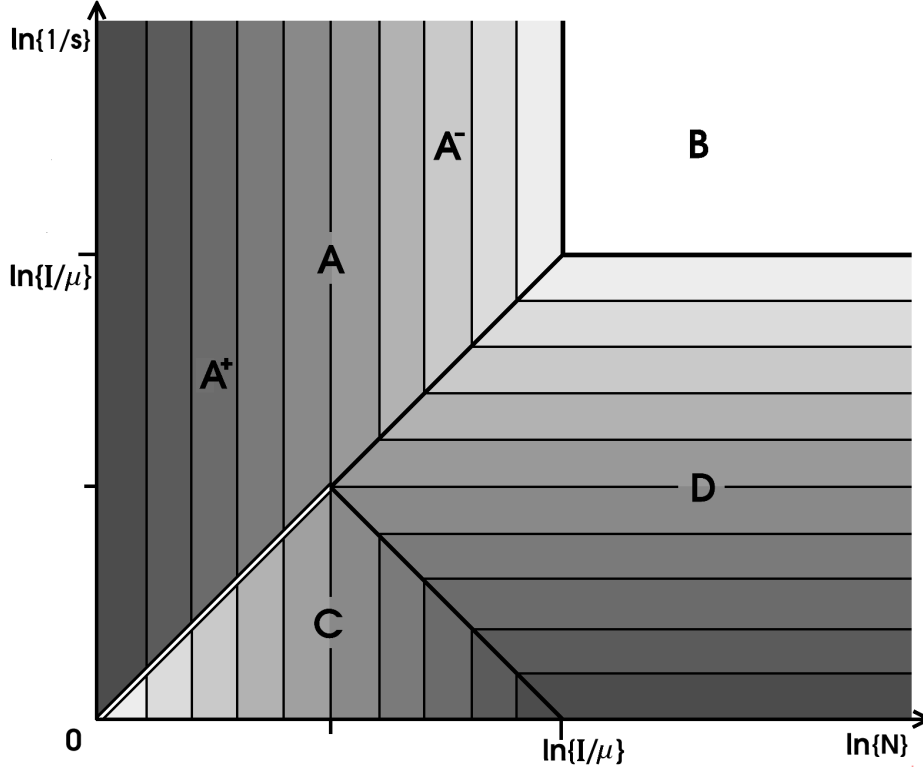
Figure 4: Evolutionary regimes: a rough logarithmic plot of the inverse of the selection coefficient s against population number N. Contours of fixed timescale are indicated by thin lines, which separate bands whose shading darkens progressively as the relevant timescale decreases. It is only in zones C and D that the Darwinian selection mechanism will be effectively operational. In zone B a stable mixed state will be approached with timescale $\tau_r \approx \tau_g I/\mu$, while in zone A there will be stochastic fluctuations with timescale $\tau_f \approx \tau_g N$, which in the subzone A^+ will go so far as to create random pure states that will last for a relatively long delay time, $\tau = \tau_r/N$, before switching. The same (delay) formula gives the timescale τ needed for attainment of the selectively preferred state in the (neo-Darwinian) zone C, while the timescale τ_s needed for attainment of the selectively preferred state in the (classical-Darwinian) zone D will be given by $\tau_s \approx \tau_g/s$. In the case of pseudo-evolution – as commonly obtained artificially – by selection of pre-existing genes, the validity of the latter (classical Darwinian) formula would extend over the zone C, thus smoothing the timescale discontinuity between A and C.

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Appendix: Crude estimation of (neo) Darwinian evolution rates

These notes recapitulate the rough and ready analysis[1] (applicable in principle to other extraterrestrial life systems, not just to our own) that I have found to be convenient as a practical working compromise between Darwin's sketchy pre-Mendelian picture of evolution and the more complete but rather too elaborate "neo-Darwinian" picture [6] that has been developed to incorporate a modern understanding of genetics.

In its simplest form, Darwinian selection for a particular bit of genetic information (e.g. a discriminator between dark or light eye colour) is describable in terms of a (small) selection coefficient s specified as the fraction by which the higher breeding rate of the favoured variant would cause its proportion of the population to increase from one generation to the next. An initially rare variant (e.g. dark eyed) could thereby become common after a number N_s of generations, and a corresponding timescale τ_s, that will be given in terms of the relevant generation timescale τ_g by

$$N_s \approx 1/s \qquad \Rightarrow \qquad \tau_s \approx N_s \tau_g. \qquad (A1)$$

Darwin's ideas about what might be achieved by natural selection in this way were largely inspired by experience of the remarkable changes obtainable in a few generations by artificial selection in species such as pigeons. However these are examples of what I would call pseudo-evolution, and as such are potentially misleading, as they depend mainly on the availability of a wealth of pre-existing genetic variation. What I would call genuine evolution requires new mutations, which will occur infrequently unless the breeding population is very large (and were first observed not in pigeons but in fruit flies).

The rate of genuine long term evolution ill be limited by the frequency of mutations, which occur as random copying errors of the genetic information I (which is carried in the terrestrial case carried by DNA coding, using just four letters, so that each inscription site involves just two bits). The (very small) probability, $r \ll 1$ say, that the code letter at a particular site will be incorrectly copied, in a single replication process, will determine a corresponding (very large) replication reliability number $N_r \gg 1$ in terms of which the timescale τ_r over which the code letter at a particular site can be expected to be replicable without error will be given by

$$N_r \approx 1/r \qquad \Rightarrow \qquad \tau_r \approx N_r \tau_g. \qquad (A2)$$

If the number, N, of individuals in the relevant breeding population (as characterised by effective diffusion of genetic information, which is achieved

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for multicellular animals by diverse sexual mechanisms) is sufficiently large, then the rate of neo-Darwinian evolution will be controlled just by the selection coefficient s and the mutation rate r. However for smaller populations the evolution rate will depend also on a third parameter, namely the size N itself, which determines the rate of occurrence of purely random fluctuations. The number of individuals carrying a particular bit of genetic information will be subject to a random walk mechanism whereby the typical change from one generation to the next can be expected to be of order $\sqrt{N}$, so that the accumulated drift after N_f generations can be expected to be of order $\sqrt{N_f}\sqrt{N}$. The expected number N_f of generations, and the corresponding timescale τ_f, needed for the drift of the fraction of the population carrying a particular bit of genetic information to become comparable with unity – so that an initally rare variant could become rare, while an initially common variant might become extinct – can thus be roughly estimated as

$$ N_f \approx N \qquad \Rightarrow \qquad \tau_f \approx N\,\tau_g\,. \qquad (A3) $$

To classify the ensuing possibilities, it is convenient – as shown in the Figure – to use a plot of N_s against N, since these parameters are variables that depend on circumstances, whereas the third relevant parameter, N_r, has a roughly constant value determined by the number I of bits of information in the genome, in terms of which the rate r of mutations at a particular site will be given by

$$ r \approx \mu/I\,, \qquad (A5) $$

where μ is the total number of mutations (per replication). Although the mutations may have external causes (such as ambient radioactivity) their rate is not passively tolerated but actively optimised by mechanisms due to long term Darwinian selection. As most random mutations are disadvantageous and many are fatal, short term individual survival requires replication reliability high enough to prevent μ from becoming large compared with unity. On the other hand a shortage of mutations would be bad for the evolutionary flexibility needed for long term survival of a species in changing circumstances, so the optimum will be given roughly by

$$ \mu \approx 1 \qquad \Rightarrow \qquad N_r \approx I \approx 10^{10}\,, \qquad (A6) $$

in broad agreement with what is observed [6].

Using the same nomenclature as in the previous discussion [1] the four main zones in the accompanying logarithmic plot of N_s against N, are labelled A, B, C, D. The simplest is the second, namely Zone B, that of weak

selection in a large population. This zone is characterised by the condition that both N_s and N should be large compared with N_r – which means that selection is too weak to matter and random fluctuations are too small to matter. In this case, after a time of the order of the value τ_r given by (A2), the population will reach a stable mixed state (e.g. comparable fractions of both light and dark eyed variants) The three other zones are more interesting.

The most unstable is the zone A, for which both N_s and N_r are large compared with N. In this zone of weak selection in a small population both τ_s and τ_r will be long compared with the timescale, τ_f, in which the accumulated effect of random breeding fluctuations can have a substantial effect. The expression (A3) for this fluctuation timescale τ_f corrects a transcription error in the original presentation [1] where the corresponding equation (4.10) was written as a copy of the formula (4.12) corresponding to (A2) above. Whenever this fluctuation timescale τ_f is short compared with τ_s there will be no time for Darwinian selection to have any noticable effect, and so long as it is also short compared with τ_r the mutation rate will be insufficient to prevent the attainment of states of a relatively pure-bred kind in which all except one of the competing variants is reduced to a very low level. Such states will remain slightly mixed in the subzone A^- for which $N \gtrsim \sqrt{N_r}$, but they will become absolutely pure (e.g. only the light eyed variant) and will then last during a relatively long delay time, given by

$$\tau = \tau_r/N \,, \tag{A6}$$

in the extreme case for which τ_f is short even compared with relevant mutation timescale τ_r/N, which will occur in the zone A^+ for which $N \lesssim \sqrt{N_r}$.

The other two zones, C and D, are those for which the Darwinian selection time scale τ_s is short, not only compared with the fluctuation timescale τ_f but also compared with the mutation timescale τ_r, the distinction being that in the former, namely zone C – the case of strong selection in a small population – the timescale τ_s is short even compared with the minimum timescale (A6) required for the occurrence of just a very few individual cases of the mutation under consideration, so that the effective limit on the rate at which Darwinian evolution can take place in the long run will be given by this minimum timescale τ, as specified by (A6).

In zone D – the case of strong selection in a large population – Darwinian selection proceeds without inhibition to eliminate all but the favoured (e.g. dark eyed) variant within a timescale of the order of τ_s as given by (A1). The

condition for this is that compared with τ_f and τ_r the selection timescale τ_s should be short, but not as short as the minimum time τ given by (A6). (The accuracy of the analysis might be somewhat improved [1] by inclusion of a factor $\ln\{\tau_r/\tau_s\}$ taking account of the mutation rate, but this will be superfluous, as it will merely be of the order of unity, unless s is extremely high.)

As shown in the Figure, there are two critical points where three zone boundaries meet. One occurs where $N_s \approx N_r$ for a landmark population number given by $N \approx N_r$. For ordinary terrestrial eukaryotes, according to (A6), this has a value of order 10^{10} that is too large to be easily attainable by large animals except in unusual circumstance – such as the impending crescendo of the human population explosion!. The corresponding timescale, τ_r as given by (A2), is in any case far too long for this triple point to be of other than academic interest except for fast breeding microbes. For large animals, with a generation timescale τ_g of the order of years, the critical value of τ_r works out to be comparable with the age of the universe and thus far too long for such evolution to have any significant effect in the relevant time window during which coherent selection tendencies can be maintained.

The other triple crossing point is more relevant for large animals. It occurs where $N \approx N_s \approx N_\times$, for a landmark population number given by

$$N_\times \approx \sqrt{N_r} \approx 10^5 \,. \qquad (A7)$$

It seems likely that the hominid population would have fluctuated about a value of roughly this order of magnitude before the emergence of our own species. Whenever the population has about this critical value the characteristic time will be given, independently of the selection rate s, by

$$\tau_\times \approx \tau_g \, N_\times \,, \qquad (A8)$$

which for animals with $\tau_g \approx 10$ years works out as $\tau_\times \approx 10^6$ years. The only relevance of the value of the selection coefficient s for such a population is that if it is too small the timescale (A8) will merely characterise random fluctuations, whereas for Darwinian selection to be effective the coefficient must satisfy the modest requirement $s \gtrsim 10^{-5}$ so that $N_s \lesssim N_\times$.

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