

“Homo informatio”

Did very “*small-world*” networks enhance the Darwinian fitness of primaeval *Homo* through exchanges of information that enabled exploration of resources beyond those exploitable at hand? An *active inference* suggestion is offered about the early evolution of human social behaviour.

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Keywords

homininan; small-world networks; mixed-sex philopatry; information; zone of bounded surprisal (ZBS); evolution

Highlights/Short Abstract

1. A broader cognitive “*zone of bounded surprisal*” (ZBS) emerged during Late Miocene times in small social units of mosaic-landscape dwelling hominins than in woodland-dwelling paninans.
2. “*Small-world*” hominin networks of very small, mixed-sex philopatric, social units, with maternal and paternal close proximity to children, facilitated the augmentation of intra- and inter-unit information.
3. Pliocene and Pleistocene spatiotemporal spread of hominins involved increases of transmissible information that expanded tool-making, resource-exploitation, and communicative fluency.
4. Biological and natural processes are indicated which could have been advantageous or disadvantageous to the survival of various hominin taxa identified in the Pliocene and Pleistocene fossil record.

Long Abstract

A phylogenetic split ~7.5 Ma (million years ago) separated paninan ancestors that were unlike today's chimpanzees, and hominin ancestors that were unlike *Homo sapiens* today; neither had evolved into their modern physical and behavioural forms. Those paninans later became mainly frugivorous woodland-dwelling *Pan* whose multifemale-multimale troops have social hierarchies where prominent parts are played by promiscuous males whose female offspring have little choice after menarche but to seek sexual partners in other troops, hostility between troops notwithstanding, whilst male promiscuity is incompatible with paternal interest in their offspring, interest being provided mainly by mothers or female alloparents.

Contrary to widespread conjecture that the aforementioned social arrangement was that of primaeval hominins, it is proposed here that by 4 Ma the nature of the mosaic landscapes (of grasslands and stands of trees) that were the habitat of australopithecine hominins, had 4 consequences that impinged on hominin evolution, differentiating it from that of woodland-dwelling paninans:

- (1) The diversity of whatever was available to eat was not the same in adjoining habitats each of which may have been constrained by whatever mostly could be foraged, scavenged, eaten, or carried away, within perhaps a 2-hour walk;
- (2) Whatever was forageable, scavengeable, and edible within that distance likely was limited at any period of the year, so social units were increasingly omnivorous and *necessarily small*;
- (3) *Smallness* demanded *cognitive ingenuity* and *transmissibility of existential information* acquired by *active inference* generated by self-evidencing through enacted neuroethological behavioural responses, in line with the free energy principle, thanks to the cognitive *broadening* of hominin “*zones of bounded surprisal*” (ZBS) with respect to *paninans'* ZBS, both *within* each hominin “*small-world*” social unit and *between* nearby hominin units spreading out, in space and time, as budding very *small-world* information networks (eventually reaching Australia and America, propagated by *H. sapiens* during the Upper Pleistocene);
- (4) The *existential continuity* of small hominin social units depended on cooperation and sporadic collaboration between social units with mixed-sex philopatry (perhaps present ~4 Ma among *Australopithecus anamensis*), behaviour which, together with (a) the generation of *information* within each unit that is enhanced by the

intimate proximity to toddlers and children of older females and males in small mixed-sex social units, and (b) mixed-sex dispersal of sexually-active partners establishing mixed-sex social units at neocalities nearby, was behaviour that maintained not only heterozygosity, but also, *crucial cognitive awareness of kinship links favouring transmissibility of information and cooperation and collaboration (rather than hostility) between neighbouring social units*, and was behaviour that represented evolutionary cognitive and social divergence from paninans.

The vulnerability of small fragile social units implies that there were hundreds of false dawns between ~4 Ma (*Australopithecus anamensis*) and ~40,000 BCE when all other hominin “palaeospecies” (including *Homo neanderthalensis*) had become extinct, leaving prehistoric *Homo sapiens* alone to roam the world, blessed with “*Homo informatio*’s” highly-evolved *hierarchically mechanistic mind* with its unequalled wide cognitive “*zone of bounded surprisal*” (ZBS) grounded in *active inference* in accord with the *free energy principle*.

TEXT

A challenging task is that of trying to reconstruct the divergent evolution of human behaviour from that of the chimpanzee, given that our last common ancestor lived ~7.5 million years ago and need not have behaved in identical ways to any of its extant or extinct successors. Palaeontology and genetics have outlined the biological (palaeobiological) trajectory of human evolution and several of its side-branches during the past four million years, thanks to field-work and laboratory research that have firm roots in rational scientific principles. These permit scientists to make retrodictive inferences that can be referred to working hypotheses on which to base further enquiry in the laboratory or in the field. Biologists are scientists who view the evolution of complex systems through the Darwinian prism of natural selection underpinning biological adaptation, including (a) evolutionary developmental (evo-devo) aspects, (b) ecological (environmental) aspects, and (c) ethological (behavioural) aspects. Such scrutiny has gained a rightful place in palaeobiology and palaeoanthropology. The latter, however, is faced with a singular biological problem, namely, how to come to terms with the evolutionary outcome of the complex, varied, open-ended behaviour that characterises our burgeoning yet single biological species (*Homo sapiens*), in a manner that keeps the evolutionary process compatible with natural selection of species, the three aspects of biological adaptation mentioned above, and the vast time-span since the last ancestor in common with the chimpanzee. A possible solution, developed here, invokes the concept of a neurobiological, cerebral, “*zone of bounded surprisal*”, relating to the amplitude of cognitive awareness and its flexibility, which is based on the formulation of “active inference” in terms of the “free energy principle”. Considerations of genetics and natural selection of species by adaptation imply imperceptibly gradual change. It is proposed that the evolutionary trajectory, of which we are the outcome, initially was made up of very *small-world* social units that fostered the transmissibility and transmission of information between members and with neighbouring units, leading eventually to major evolutionary changes that came to characterise human biology and human behaviour. As with alternative proposals that interpret the changes from an actualist standpoint, based on comparison or contrast with contemporary ape behaviour, the proposal lacks empirical Pliocene instantiation, while offering a scientifically plausible rationale.

1. Introductory Background

The earliest known fossils of our human genus *Homo* come from East Africa and are nearly three million years old (~2.8 Ma; shortly before the transition ~2.58 Ma from the Pliocene epoch to the Pleistocene). *Homo* became the sole surviving hominin genus after ~1.3 Ma of those habitually-bipedal Hominini which included *Australopithecus*, *Kenyanthropus*, and *Paranthropus*. Palaeoenvironmental considerations suggest that the habitually-bipedal forms exploited landscapes that were of less interest to quadrupedal hominins, given the dearth of fossil ancestors of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) - two quadrupedal African hominin species that genetics implies had separated by ~2.0 Ma, though no *Pan* fossils are known before ~0.6 Ma. By contrast, fossil gelada baboons (*Theropithecus*) are present in some sediments containing bipedal hominin fossils [1] [2] *cf.*[3]. Genetic comparison implies that the last common ancestor of humans and chimpanzees lived ~7.5 Ma in the Late Miocene *cf.*[4]. The Hominini and Gorillini are taxonomical tribes of the hominine subfamily Homininae that, alongside the Ponginae (orangutans), composes the great-ape hominid family Hominidae [5] that along with the Hylobatidae (“lesser apes”, gibbons) makes up the hominoid superfamily of Hominoidea of tail-less Primates, whereas monkeys, including geladas, mostly have visible tails.

In East Africa during the Early Pliocene, the perhaps sporadically bipedal *Ardipithecus ramidus* persisted ~4.2-4.1 Ma when it may have been a neighbour of the early, habitually-bipedal *Australopithecus anamensis*, co-existing in a mixed landscape of grassland and woodland that could allow the perpetuation of arboreality alongside the exploitation

of open country. Previously, the ~5.5 Ma *Ardipithecus kadabba* dwelt in a more wooded environment, as probably did the somewhat earlier fossil hominines, *Orrorin tugenensis* and *Sahelanthropus tchadensis*, and the even earlier (9.9-9.8 Ma) hominid *Nakalipithecus nakayamai* that perhaps was among the ancestors of *Chororapithecus abyssinicus* (~8.5-7 Ma) that may have been a fossil precursor of modern Gorillini whose troops of between 5 and 30 members exploit humid woodland. *Australopithecus* was a widespread genus, present ~3.5 Ma not only in East Africa, but also beside the Central African Lake Chad (today ~300 m a.s.l.), and even on the South African Highveld karst (today ~1,400 m a.s.l.) which it shared with *Paranthropus*, and, much later on, *Homo* ~1.8 Ma. Skeletal remains of the obligate biped *Homo* come from Transcaucasia ~1.8 Ma, though sites with stone artefacts or evidence of anthropic activity in North Africa, the Near East, Europe, Russia, and China have dates ≥ 2 Ma [6] [7] [8] [9], implying early widespread homininan dispersals across diverse landscapes. Adaptive behavioural responses by habitually-bipedal hominins, but which are uncharacteristic in *Pan*, seem to have been present ~3.4-3.3 Ma when stone-flaking and cut-marked bone offer East African evidence from half-a-million years before there are skeletal remains assignable to *Homo*; maybe stone-flaking was done by penecontemporaneous *Kenyanthropus platyops*, possibly a close antecedent of *Homo*, but *Australopithecus* and *Paranthropus* were likely capable also.

From the contrastive behavioural and ethological standpoints of dynamical evolution, a two-way division of the Hominini tribe into subtribes of Panina (paninans; *Pan*) and Hominina (homininans: *Australopithecus*, *Kenyanthropus*, *Paranthropus*, *Homo*) is convenient. A three-way division is preferred by some palaeoanthropologists who reserve the subtribe Hominina exclusively for *Homo* and assign other extinct habitually-bipedal genera to an australopithecine subtribe (Australopithecina) [10] [11] [12]. The anatomical rationale for a tripartite arrangement could well be appropriate for an australopithecine clade with characteristic behaviour in which bipedalism went hand-in-hand, or hand-and-foot, with climbing up trees, or on to narrow edges of steep rock outcrops or cliffs, for nesting, resting, and observing predators at a possibly safe distance. Given the likelihood that such activities were among behaviours achievable by *Homo* 3 million years ago, the two-way paninan-homininan distinction seems appropriate, and henceforth *homininan* is used to embrace australopithecines and Early Pleistocene *Homo*. Despite a widely-held view that African homininans likely were frequent victims of predatory creatures [13] [14], only very few African excavated sites that were feeding places or lairs of large carnivores provide indisputable taphonomical evidence of osteological damage inflicted by them on Plio-Pleistocene homininans (e.g. [15] [16] [17]). Moreover, osteological damage sometimes could be an outcome of the removal by a scavenging carnivore of a fresh corpse (not necessarily one that it had killed), in order to eat it, or share it with offspring, somewhere unattractive to competing scavengers.

Early analyses of trace-elements and stable radiogenic isotopes in bones and teeth from the Swartkrans palaeocave site, in South Africa, implied both that predators had devoured robust australopithecines and *Homo erectus-ergaster* there, and also that those homininans had fed on a range of plants and, plausibly, small vertebrate and invertebrate prey [18]. Subsequent analytical research has shown that *Australopithecus* and *Paranthropus* homininans sampled in southern Africa had a dietary range, including not only components derived from the C₃ photosynthetic pathway but also some from the C₄ pathway, which was wider than that of other Plio-Pleistocene Primates there, and reflected “a broad ecological niche” [19] (though carnivores seem to have eaten some of them), and that perhaps there was female dispersal [20] [21]. Because the C₄ pathway is widespread in dry landscapes (e.g., savannah grassland), eating plants in them (e.g., sedges and their edible tubers or rhizomes; tropical grasses) or parts of animals that feed on those, indicates aspects of the environment, and may point to the eater’s rank in the trophic food chain of an ecosystem. It is important, nevertheless, to remember that in the Kenyan Turkana basin the earliest homininan, *Australopithecus anamensis* (4.3-3.8 Ma), mainly ate C₃ foodstuff [22] like the non-homininan hominines. Isotopic research in the Ethiopian Lower Omo River basin shows that after 2.4 Ma there was an increase both in the intake of C₄ plants by grazing animals and in the intake by homininans of such plants or of food derived from such animals [23]. In the Ethiopian Awash River basin there existed four palaeontologically-distinct homininan taxa between 2.8 and 2.5 Ma [24]. Continent-wide climatic changes, palaeoecological variability between and within regions, and differences in feeding proclivities between or within homininan taxa, all complicate attempts to identify when, where, and which homininan species rose to the rank of frequent eaters of food extracted from animals that graze on C₄ vegetation, and whether access was gained by homininan scavengers or hunters. The matter is of interest not only from the broad viewpoint of human evolution within the Homininae, but also with regard to the evolution in the Hominina of the brain, cognition, and use of information. Given the dental, maxillo-facial, and general skeletal features that separate the taxa *Australopithecus*, *Paranthropus* and *Homo* from one another, and the presence of the three taxa in broadly similar African landscapes at the onset of the Pleistocene (2.58 Ma), a plausible conjecture is that their respective patterns of routine behaviour were not precisely identical to one another, much less were they identical to those of any extant Homininae. Another plausible conjecture is that natural selection of adaptations affecting behaviour took place successively, through gradual genetic neurobiological modification, in three long spans of geological time. The first was from ~7.5 Ma to the appearance in

the fossil record of *Australopithecus anamensis* ~4 Ma, when the second time-span began which embraced the appearance successively of *Paranthropus* and *Homo*, and lasted until ~2.3 Ma *cf.*[25].

The third time-span saw the disappearance of *Australopithecus* and *Paranthropus* and the dispersal of *Homo* into Eurasia, and by ~0.77 Ma (the onset of the Middle Pleistocene) the behaviour of *Homo* had little in common with the routine behaviour of contemporaneous taxa of Homininae. The first time-span lacks tangible finds of behaviour that can be attributed unambiguously to *Australopithecus* or any other hominin. From the second, cut-marks on bone [26], flaked stones, [27] [28] [29], and transport of stone [30] indicate hominin activities that are not undertaken routinely by extant wild Hominidae. Stone core-and-flake assemblages, uncharacteristic of behaviour by modern great apes, represent the earliest Palaeolithic technology which often is designated Oldowan (after sites at the Olduvai Gorge). Whilst *Australopithecus* might have performed core-and-flake activities in various parts of Africa, in East Africa *Paranthropus* and *Homo* are especially plausible protagonists [31]. Flaked stones from Gona (Ethiopia), ~2.6 Ma, imply the existence of manipulative skills that were intermediate between those of trained chimpanzees or bonobos and human trainers [32]. At the onset of the third time-span, stone was being knapped at the 2.34 Ma site of Lokalelei 2C (West Turkana, Kenya) with an accuracy and precision [33] [34] rarely reached, if ever, by extant paninans trained by stone knappers.

Thereafter, the Palaeolithic record provides noteworthy evidence of undoubtedly hominin behaviour. This is manifested not only by different repeated forms of artefacts such as hand-axes, cleavers, retouched regular flakes, and spheroids, which are made by incompatibly unique sequences of the manual reduction of stone or bone *cf.*[35] [36], but also by attention to fire and perhaps the roasting food, long before evidence of pyrotechnology is present in the Palaeolithic record, *cf.*[37] [38] [39] [40], and by geographical dispersal into Eurasia [6] [7] [8] [9], though some of the behaviour could have been that of not only *Homo* but sometimes also *Australopithecus* or *Paranthropus* in Africa. Sections 2 and 3 provide the basis of the conjectural argument from the standpoint of neurobiological cognitive evolution (of “zones of bounded surprisal” in line with *active inference* according to the *free energy principle*, see Section 2), but it is enough here to state that the three spans of time correspond to, first, the bio-behavioural and genetic seeds of propensities that, secondly, initiated the widening of explorative behaviour and epistemic awareness of alternative possibilities for taking appropriate actions, which, thirdly, enabled their successful various and varied undertaking (e.g., hunting, trapping) without impairing reproductive success (a.k.a., adaptive fitness, Darwinian fitness). A matter of surmise concerns just what factors impaired the reproductive success of *Australopithecus* and *Paranthropus*, hindering their survivability, and leading them to extinction.

Much has been written about human or Primate victims of predatory carnivores and the possible implications for the survivability of Plio-Pleistocene hominins. Palaeontological considerations [41] [42] [43] indicate that the East African carnivore guild underwent a decline after the appearance of *Homo erectus* (*ergaster*), who could have contributed to it, perhaps more by scavenging than by hunting. Before that time, Plio-Pleistocene hominin behaviour could have involved sporadic stealing of food from carnivores’ feeding places, but its likely infrequency, on account of confrontational risks during such scavenging, might favour a consideration of hominins as primary predators [44 p. 365]. It is doubtful that hominin organisation in Pliocene landscapes resembled that of today’s woodland chimpanzees or bonobos, “because the risk of conspicuousness and the added costs of vigilance in large, competitive parties would have been prohibitive in the carnivore rich terrestrial habits (sic) under consideration... (This) conjecture leaves open the possibility that hominins formed quiet, cohesive groups with less distracting competition” [44 p. 369] “...shaped strongly by inter-individual proximity and social relationships. Therefore, safety may depend on establishing familiarity, trust, and reciprocity with a few individuals who will warn others when a predator is detected” [44 p. 369]. According to that reasonable interpretation, the *smallness* of the social units enhances the transmission of information. Narrow edges or shelves on steep rock outcrops or cliffs, and dispersed, small stands of trees for nesting, could have accommodated very small hominin social units only, though such places that were within easy walking distance of each other could have enabled social units to exchange kin, cooperate, and collaborate sporadically in joint activities that may have involved two, three, or sometimes even four social units, coming together from time to time.

Undeniably, the absence of dense arboreality and the world-wide presence in diverse natural surroundings render unique the *adaptive zone* of contemporary *Homo*. Nonetheless, within both *Australopithecus* and *Paranthropus* the anatomical descriptions of morphologically-distinctive fossil “palaeospecies” hardly imply that these became, so to speak, dead-end “twigs” on an evolving hominin figurative “bush”. Plausibly, this *uncommon diversity of osteologically-discrete forms within the hominine fossil record* reflects a *common hominin evolutionary tendency* towards the development of neurobiological mechanisms that enabled and enhanced the hominin exploration and exploitation of a *diversity of environments* unattainable by paninans. An inverse temporal relation may exist between the decline of the African large-carnivore guild and the expansion of hominin brains, which perhaps reflects growing

homininan impingement on ecosystems [45] and, quite possibly, the growth of the homininan population, together perhaps with its existential behaviour conditioned by increasingly seasonal environmental fluctuation, such that, after ~1.75 Ma large carnivores no longer enjoyed their previously unrestricted access to ungulate prey [46] [47].

A plausible conjecture is that some homininan very *small-world* social units were capable of collaborating in joint enterprises, such that their epistemic “lore”, or neurobiological cognitive awareness about their environments, enhanced the exploitation of these and, in consequence, enhanced reproductive success. The palaeoanthropological record indicates that, in this regard, the genus *Homo* was more successful than *Australopithecus* first, and, finally, *Paranthropus* with which it coexisted until ~1.5 Ma. A widespread inference from the Early Pleistocene Palaeolithic record is the implication of *Homo* with the evolution of technical aptitudes from ~1.75 Ma and with the demographical spread ~2 Ma into Eurasia, both of which suggest that the adaptive fitness and reproductive success of *Homo* outstripped those of *Paranthropus*. However, not even in the Early Pleistocene can stochasticity and ergodicity be overlooked when considering Palaeolithic behaviour [48], as British archaeologists have long been aware *cf.*[49 esp. p. 262] [50 esp. p. 28] [51 esp. p. 186].

It is proposed here that the failure of several homininan taxa to attain and maintain the reproductive success necessary to avert their extinction cannot be attributed mainly to ecologically-driven differentiation, because the identification of different taxa in Pliocene and Early Pleistocene sedimentary contexts which often were similar implies that their natural surroundings were more or less commensurate. This situation likely continued even when the environments were undergoing geologically-speaking quite rapid environmental evolution of ecotones and the corresponding biotopes. Put in technical jargon, the undoubted skeletal differences between penecontemporaneous homininan taxa cannot easily be explained away by a conjecture that they were biologically-specific outcomes of different morphological or physiological adaptations to their supposedly respective evolving *adaptive zones* that were supposedly *specifically-unique fitness landscapes*. It is likely that often there existed overlapping ecological characteristics of several adjacent territories exploited by anatomically-defined homininan taxa whose diverse morphological aspects owed to inherited differences that only with imaginative hindsight might be conjectured, perhaps, as being inevitably predictable outcomes of the differential natural selection of morphological modifications to supposedly different, albeit unidentifiable, environmental components. The argument to be developed here is that gradually-evolving *behavioural* differences between homininan taxa underlay long-term differences in their survivability and evolvability.

Notwithstanding their diagnostic osteological differences, some Plio-Pleistocene homininan taxa seem to have been penecontemporaneous and able to exist in quite similar surroundings, which suggests they shared at least some behavioural abilities that differed markedly from modern paninan behaviour. Granted the foregoing, a not unreasonable surmise is that heritable bio-behavioural *Baldwin effects* (e.g., transmission of learnt or acquired responses to novel

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***Baldwin effect:** an evolutionary process where a behaviour, learnt by experience and developmental plasticity, becomes genetically hardwired and instinctive over generations by natural selection, such that those creatures that are better than others at learning and adapting to new traits and environments have a greater chance of reproducing and their offspring inherit the underlying genetic predisposition for the learnt behaviours, that may become innate. Developmental plasticity is thought to speed up the biological evolution of traits that favour reproductive success (adaptive, Darwinian fitness). The concept was foreshadowed by Charles Darwin's acquaintance the biologist Douglas Alexander Spalding [52] *cf.*[53], and twenty years later on was it developed and promulgated by the psychologist James Mark Baldwin [54]. A computational demonstration of the plausibility of the *Baldwin effect* [55] was at first well received *cf.*[56], but latterly methodological shortcomings have been detected [57]. A recent simulation study [58] indicates that the mechanism of plasticity with regard to behavioural acquisition or learning is a significant determinant of heritable *Baldwin effect* outcomes.

information involved in niche-construction [59] [60] *cf.*[61] [62], or other numerical aspects (e.g., birth spacing), influenced differentially the evolutionary rates of selective adaptations of the population structures of different contemporaneous or penecontemporaneous homininan taxa. Frequency-dependent variation between groups in their rates of births and ages of reaching sexual maturity can lead to differences between successive generations which affect

their respective genetically-effective demographical sizes, with possibly long-term evolutionary consequences for morphology. With regard to Late Pliocene hominin taxa, variations could have been brought about initially by way of variable behavioural impingements that imperceptibly affected different small groups differentially according to the extent to which learnt practices became established within some groups by their ability to consolidate information. Plausibly, such processes influenced morphology variably, both directly through genetic inheritance of anatomical characteristics, and indirectly throughout ontogenetic development. The relative reproductive success of hominin “palaeospecies” likely depended on the interplay of the various influences, forming, as it were, a race between evolvability and survivability, with unpredictable outcomes. A possibility (see below) is that a *neuroethological* approach could be appropriate for interpreting the dynamical mechanisms that likely impelled hominin evolution, ontogenetic development included, towards increasingly-complex handling of information in and between social units that were exploring and exploiting their surroundings. The mechanisms are related to fundamental matters of general neuroscientific interest.

During the Late Pliocene, hominins seem to have been able to explore and exploit a wide range of landscapes. They may have preferred moist grasslands and humid woodlands in an ecological patchwork that offered a broad diversity of bioenergetic resources, whilst also foraging on rough slopes and karst. Bioenergetic resources were limited both by seasonal availability and competitors. Conceivably, advantage can be gained over competitors by expediting whatever exploratory news most efficaciously enables epistemic awareness of versatile exploitative strategies. Here, it is advantageous to maintain an open-ended attitude towards envisaging pragmatic, agile, alternative possible tactics in addition to customary ones. Expeditious use of novel information is possible when there is continual social intercourse within and between very small, agile, neighbourly units that are related by kin. By contrast, appreciation is hampered if new information is diluted when filtered through a bustling pack or noisy panin troop. Such a troop may constrain the appreciation of contributions from young members whose learning, in turn, may be constrained by a social hierarchy preoccupied with steering a seasonal round within its territory, keeping prudent distance from other troops, and eschewing reciprocal exchange of kin with them, albeit motivating emigration by its post-menarcheal young females as occurs among wild chimpanzees [63] [64].

A plausible evolutionary conjecture is that, over a few million years, from the Pliocene into the Early Pleistocene, hominin behaviour, evolved through the slowly increasing versatility of tiny, contiguous, familial social units (e.g., Table 1), each consisting of barely a dozen members, including an alloparental individual (e.g., elder sibling, grandparent, aunt, uncle, cousin, nephew, niece, friend, neighbour, colleague, etc.), present together at any one time, whose reciprocal exchange of kin of both sexes produced mixed-sex philopatry. Several Primate taxa, including Hominidae, show *within-species diversity* as regards not only size or territorial range, but also composition by age, sex, and philopatry of groups or sub-groups [65], and human philopatric variability is documented for some contemporary hunter-gatherers [66]. Behavioural flexibility likely evolved gradually in Primates (monkeys and apes especially, from the Oligocene onwards) hand-in-glove with the evolution of the flexible processing and transmission of environmental information. Late Pliocene hominin social units co-existed and seem to have evolved in mosaic landscapes. By contrast, from the Late Miocene onwards, panin behavioural ecology and ethological responses could have evolved towards an ever-increasing social-unit size that in *Pan* nowadays is of ≥ 20 or sometimes > 50 members, living mainly in woodland suitable for regular frugivory, folivory, herbivory, insectivory, and sporadic carnivory. A not implausible conjecture is that, between ~ 7.5 and ~ 3.5 Ma, divergence took place away from whatever demographical situation had characterised the Miocene common ancestor of panins and hominins, such that panin social units evolved to become each more numerous than it – forming troops, while hominin social units evolved to become each less numerous than it – forming very small social units. In consequence, during those four million years, specific differences evolved in the relationships between individuals, such that heritable behaviour, and maybe even genetically-inherited behavioural propensities, began gradually to separate hominin from panin customary behavioural patterns. Vis-à-vis panins, “*small-world*” hominin social units could well have favoured “...motivational changes. Parents might become more tolerant of juveniles in close proximity, and tolerant of them experimenting... Juveniles might become more focused on adult activity” [67 p. 33]. Imperceptibly slow demographical evolutionary divergence could answer the question [68] of what seeded the emergent evolution of human behaviour.

Hypotheses of Late Pliocene hominin emergence from Early Pliocene and Late Miocene hominin ancestors are based often on evolutionary proposals about adaptive fitness that are drawn in a 20th-century, methodologically-uniformitarian way – i.e., assuming *other things to have been equal* – from reasonable contemporary considerations of adaptive biological and ethological responses to the environmental availability of those bioenergetic resources that afforded not only least-effort sustainability but also enabled repeatability of primaevial hominin and hominin life-cycles. Such methodological considerations have provided noteworthy lucid analyses, e.g.[69]. Research taking this paradigmatic approach abounds in primatology, ethology, biological and physical anthropology, behavioural

anthropology, palaeoanthropology, palaeobiology, human palaeoecology, and prehistoric archaeology. The approach has inspired countless publications, research papers, and unpublished dissertations. Nevertheless, often insufficient attention is paid to geologically- or geomorphologically-related effects (*e.g.*, in East Africa) that could require re-evaluation of several published scenarios, because they impinge on palaeoenvironmental evolution and palaeontological sampling [70] [71] [72] [73].

Those effects imply the possible inappropriateness or incommensurability of analogical inferences, drawn from observations about behaviours recorded in apes, monkeys, or other creatures, whether in captivity or in the wild, that are widely held as providing us with substantive uniformitarian principles on which to base methodological uniformitarian interpretations about Plio-Pleistocene wild-life. Prudence cautions against trying to squeeze Holocene ethological pegs into Plio-Pleistocene palaeoathological round holes. Such inferences may be no more than "false analogies" and no less imprudent than are other possibly "false analogies" drawn from historical or ethnographical accounts of hunter-gatherers' behaviour that, by "top-down" reasoning, is inferred, analogically, as being suitable, at least in part, for transposition on to the incommensurate and incommensurably spatiotemporal vastness of the Pliocene and Early Pleistocene Old World without prior need for us to re-set the focus of *time-perspectivism* [74] [75] [76] [77] [78], away from a focus on contemporary behaviour in discrete localities of recent human foragers or hunters, *cf.*[48] [79] [80].

The matter is not trivial. From the standpoint of statistical mechanics and thermodynamics, developed during the nineteenth century and giving rise in the twentieth to recognition that the transmission of information is based on physical concepts which relate also to the *free energy principle* and *active inference*, theoretical physicist Carlo Rovelli [81 p. 198] explained that "... time is not a fundamental constituent of the world, but it appears because the world is immense, and we are small systems within the world, interacting only with macroscopic variables that average among innumerable small, microscopic variables... We, in our everyday lives, never see a single elementary particle, or a single quantum of space. We see stones, mountains, the faces of our friends – and each of these things we see is formed by myriads of elementary components. We are always correlated with averages. Averages behave like averages: they disperse heat and, intrinsically, generate time. The difficulty of grasping this idea comes from the fact that it is hard for us to think of a world without time, and of time emerging in an approximate manner. We are too used to thinking of reality as existing in time. We are beings who live in time: we dwell in time, and are nourished by it. We are an effect of this temporality, produced by average values of microscopic variables. But the limitations of our intuitions should not mislead us. Understanding the world better often entails going against intuition. If this were not the case, understanding would be easy. Time is an effect of our overlooking of the physical microstates of things. Time is information we don't have."

Ay, there's the rub! The above quotation is preceded by "Whenever you consider a phenomenon certifying the passage of time, it is through the production of heat that it does so. There is no preferred direction of time without heat. But heat is our way to name averages over many variables. The idea of thermal time reverses this observation. That is to say, instead of enquiring how time produces dissipation in heat, it asks how heat produces time. Thanks to Boltzmann, we know that the notion of heat comes from the fact that we interact with averages. The idea of thermal time is that the notion of time, too, comes from the fact that we interact only with averages of many variables. As long as we have a *complete* description of a system, all the variables of the system are on the same footing; none of them acts as a time variable. That is to say: none is correlated to irreversible phenomena. But as soon as we describe the system by means of averages of many variables, we have a preferred variable that functions like common time. A time along which heat is dissipated. The time of our everyday experience" [81 p. 198].

From the standpoint of considering evolution, "...in physics there is no clear definition of a complex system, but there is a clear definition for a dissipative structure. And, in dissipative structures, complexity is an integral part. This complexity in dissipative structures appears in terms of the composing network of thermodynamic forces and flows... Emergent force flow couplings can provide novel organizational states for a dissipative structure. If these novel processes and configurations affect the stability of the system, they can be selected for. A schematic of natural selection can thus be inferred as a process of fluctuation-induced emergence of dynamics (*i.e.*, mutation) leading to differential self-maintenance dynamics (*i.e.*, phenotypic differentiation) that are selected for by the embedding circumstances (*i.e.*, adaptability). The complexification of organic life by evolution need not appeal to statistical or morphological measures of complexity, but rather can be indexed by the network of thermodynamic force–flow couplings and the related multiplicity of organizational states" [82 p. 115].

With regard to the complex processual relationships between biological and behavioural evolution, there are severe limitations to the applicability of retrodictive hypotheses inferred from "average" actualist conclusions drawn

from contemporary ecology and ethology (e.g., about feed-back and feed-forward behavioural “loops”), and prudence counsels against a sanguine interpretation. Climatic and environmental changes that may occur within a millennium, or even a century, often are mostly unrecognisable before the onset of the Middle Pleistocene (~0.77 Ma) in palaeontological, palaeoanthropological, and Palaeolithic records from before ~1 Ma, during the previous 6.5 million years from the last common ancestor of chimpanzees and modern humans that lived ~7.5 Ma.

In order to envisage the Late Miocene and Pliocene appropriately, the focus of *time-perspectivism* implies giving consideration to a plausible contrast, in open landscapes containing large predators, between, on the one hand, the likelihood that sizeable troops (e.g., of geladas) allow reproductive continuity to succeed more often, and with greater long-term stability, than might be the case for small groups that are easy prey, and, on the other, the long-term *evolution by natural selection* of a plausibly emergent hominin propensity to incremental cognitive and behavioural versatility by living in very small social units, whose newborn members were exposed to a wide variety of the different “*small-world*” behaviours of surrounding members of both sexes and all ages (in their own and sometimes in neighbouring kinship social units), such that from birth onwards they increasingly were able to gain discriminatory awareness about that behavioural variety by giving it their attention and scrutiny. Both are “middle-range” (cause-effect) theories. However, the first is based on the actualist premiss that past circumstances should be regarded as having been commensurate with present ones until there is overwhelming substantial empirical evidence to the contrary. The second is more cautious, because it keeps in mind the underpinning of physics, that is common to past and present circumstances. Therefore, it enjoins prudence on us before we presume that uncertainty about the past, and about those processes that developed in it, can be brushed aside (*pro tempore*, at least). It fails to acknowledge that uncertainty is a condition or circumstance during and throughout biological evolutionary processes, not just an intellectual problem that worries some scholars more than others. The intrinsic uncertainty of models based on uniformitarian premisses is what underlies proposals that invoke wider ranging palaeoethological theories, notwithstanding the gaps that uncertainty may never let us bridge.

From the aforementioned considerations, plausibility can be assigned to the notion put forward here that, by natural selection, an emergent hominin propensity towards human behaviour enabled a gradual expansion of the phylogenetic hominin “*zones of bounded surprisal*” (ZBS) [80], by *active inference* in accord with the *free energy principle* (see below and Section 2). Because this *first-principles* interpretation implies an *ultimate* explanation in line with natural selection in the origin of species, it offers an advantage, and perhaps a theoretical advance, over *proximate* explanations such as regarding different phylogenetic social behaviours of Simiiform Primates as somehow being consequent on how their various species' respective mean differences of cerebral mass may be correlated, *other things being equal*, with their mean social-group sizes or perhaps with their fecundity. Instead, the interpretation proposed here is that the evolution of social behaviour took divergent evolutionary paths in paninans and homininans after their last common ancestor of the Late Miocene. In the hominin evolutionary trajectory there developed genetically- and epigenetically-established adaptive *evo-devo* mechanisms involving neuroethology and ontogeny. A significant outcome of the neurobiological ontogenetic evolutionary divergence is the phylogenetic differentiation of *zones of bounded surprisal* (ZBS) that today separates humans from chimpanzees and bonobos.

But what if some things had *not* been equal? What if something lacking in the transposition of substantive uniformitarian conclusions to a methodologically-uniformitarian principle could be an *additional* consideration of the likelihood of *differential diachronic (time-wise) evolvability of those biological and ethological responses* which need not have developed at one and the same, constant, invariant rate in each and every hominine and hominin taxon between ~7.5 and ~1 Ma?

Against the notion that the size of Pliocene hominin social units could have been similar to that of paninan troops today, it should be pointed out that much evidence adduced to support it is open to question. Claims that the increments in hominin skull volumes overall, from the Late Pliocene to the Late Pleistocene, are *per se* reliable indicators of increasing sizes of individual prehistoric social groups (let alone, of their allegedly “cumulative cultural” complexity) fail to take due account of *time-perspectivism*. The claims put the cart before the horse by presuming that for which scientific enquiry ought first to have provided substantive evidence that can withstand sceptical rebuttal. Palaeontological evidence is lacking that might lend support to a surmise that during the Late Miocene the last common ancestor of the paninans and homininans lived in social units with numbers of members similar to those of today's chimpanzee troops. It is a postdictive or retrodictive surmise, also, that the size of Plio-Pleistocene hominin social units was similar to that of today's (Late Holocene) *bands* of hunter-gatherer kin-related social units. A house of cards can be built up by the ill-advised application of an allegedly biologically-based substantive uniformitarian account of present-day reality by transforming it into a methodologically uniformitarian programme for Late Caenozoic ancestors of paninans and homininans. This ignores not only the immense ecological changes that were transforming Africa

throughout the Late Miocene and Pliocene, and to which the various descendants of the last common ancestor had to adapt (and which unquestionably evolved, otherwise there would be neither chimpanzees nor humans alive today), but also the absence of incontrovertible Palaeolithic or palaeontological evidence (*in contra* to that for fossil *Theropithecus*) that could give us a strong clue about the inferable social-unit sizes of paninans and hominins before the start of the Late (Upper) Pleistocene (*i.e.*, before ~0.13 Ma). On the other hand, what we do know is that, unlike paninans, hominins before 3 Ma already were present not only in East Africa but also in South Africa and Chad, and by 2 Ma in North Africa, the Near East, Europe, Russia and China [6] [7] [8] [9], all of which suggest some cognitive abilities of bipedal creatures whose brains, albeit smaller than most of ours, enabled them nonetheless to move to and survive in environments that were not only different from those of today's chimpanzees and bonobos but also different from those in which and to which already the earliest hominin (*Australopithecus anamensis*) had become adapted ~4.2 Ma. The foregoing considerations suggest that appropriate proposals about social-unit size are in order which can be referred to theoretical principles, such as the free energy principle and active inference, underpinning the hominin evolution of *hierarchically mechanistic minds* (see below), and which can be accommodated within a minimal "bottom-up" interpretation of such empirical paleoanthropological and Palaeolithic evidence as may be uncontroversially knowable about hominin behaviour during the time-span under review, whilst being an interpretation in accord with contemporary biological understanding about the *extended evolutionary synthesis*.

Today, the *differential evolvability* of two lineages descended from a last common ancestor is an unproblematic concept from the 21st-century viewpoint where the erstwhile 20th-century *modern* or *neo-Darwinian* evolutionary synthesis (between Mendelian allelic genetics underpinning the adaptive fitness of organisms, and allelic population genetics underpinning the selection of species from them) has evolved into an ("evo-devo") *integrated* or *extended evolutionary synthesis*, in order to take into account significant contributions of epigenetics, evolutionary developmental biology or ontogeny, niche-construction, and the dynamically-evolving *interaction* of *all* components of any environmental niche when regarded from a not impossible theoretical standpoint (see Section 2) of *quantum reference frames* borrowed from quantum field theory. A particular concept of noteworthy evolutionary relevance to behaviour and learning in mammals, and perhaps birds, is that of *hierarchically mechanistic minds* [83] [84] [85] *cf.* [86] [87] [88]. It is based on *active inference* [89] [90] [91], in accord with the physical *free energy principle* [92] [93]. The concept is applicable to the biological evolution, through natural selection, of the behavioural consequences of species-specific adaptations of neurobiological predictive coding mechanisms [94] [95] [96]. Among such adaptations are *zones of bounded surprisal* (ZBS) [80] for which a crude analogy is that of band-pass filters. The human ZBS is broader than that of paninans; their remarkable cognitive abilities pale before the vast range of human open-ended thinking. In the hominin lineage, the evolution of hierarchically mechanistic minds towards precise and accurate epistemic appreciation of practicable exploitative outcomes is explicable from the standpoint of active inference and neuroethological information received from and transmitted to seamless natural-cum-social environments *cf.* [97] [98] [99] [100] [101] [102] [103]. It is proposed here that a matter of likely relevance is the part that was played by "*small-world*" relationships in hominin evolution, especially by the *transmission of information* in and between evolving neighbouring "*small-world*" networks, which plausibly impinged on the *differential evolvability* in hominin vis-à-vis paninan phylogeny after ~7.5 Ma.

2. Information transmissibility

Regarding the efficient transmissibility of information when social unit size is very small, it is of tangential interest that, from the standpoint of model gene-culture coevolutionary allelic considerations, which relate to *W.D. Hamilton's rule** about the conditions under which inclusive fitness can result from kinship selection, the statistical

* ***W.D. Hamilton's rule*** holds that an "altruistic" act is favoured if $rB > C$, where r = the proportional genetic relatedness between an "altruistic" actor and its recipient (thus, a parent and child share 50% of their genes, hence $r=0.5$, whereas siblings share a similar degree of relatedness; B = benefit gained by recipients in terms of reproductive success (*i.e.*, number of offspring); C = cost to an "altruistic" actor, estimated in terms of his or her own reproductive success (*i.e.*, number of offspring begotten). The rule implies that individuals likely will help a close relative, who share genes with them, and, thus, if the indirect genetic benefits of helping a close relative outweigh the direct costs to an individual, then his or her altruistic behaviour will become selected genetically in that social unit, when repeated over several generations [104].

probability of contingent cooperative attitudes among individual members – as against punishable uncooperative ones – is greater in tiny human groups (*e.g.*, ten people) than in bigger ones (*e.g.*, 100 people) when both groups are subject to equivalent rates of immigration by ethnolinguistically assimilable non-kin, though selection is perforce weak and remains so even when the small groups are envisaged within a social landscape of neighbouring ones with whom kin

may be exchanged *cf.*[105]. However, this hardly can have been the social landscape of Pliocene or Pleistocene hominins, let alone that of the very first of these; indeed, the likelihood of demographical sparsity renders it hard to envisage the existence of such a social landscape before half-a-million years ago.

Moreover, behaviours, whether of cooperative adults or of uncooperative punishable adults, are not directly commensurable with their respective emission, transmission, or receipt of information about admissible or inadmissible behavioural responses. Those matters also depend on individual ontogenies and post-natal upbringing, throughout which exchanges of information between developing children and members of their families or other individuals mould a diversity of personal outcomes in the attitudes and behaviours of human adults. It is important to stress that it is precisely the eusocial *bi-parental* cooperative behaviour in the provisioning and upbringing of offspring in monandrous mating systems which distinguishes human behaviour from that of paninans. The following authoritative statement [106, p. 53] is relevant: “*Among both invertebrates and vertebrates, cooperative behaviour between unrelated individuals that are not potential breeding partners is seldom highly developed even if they live in stable groups or colonies. Most of the more costly forms of cooperative behaviour, such as the provisioning of young born to other individuals, are restricted to species living in groups consisting primarily of relatives. For example, cooperative or eusocial breeding appears to be restricted to lineages with monandrous mating systems, which generate relatively high levels of relatedness.*” It also should be borne in mind that not even the genetic underpinnings of a species’ archetypical behaviour are necessarily immune to a *Baldwin effect* or its possible consequence for cooperation [107]. Perhaps one outcome of a *Baldwin effect* could be the modification of the internal *breeding structure* of *small* social units. The likelihood of their extinction notwithstanding, in a surviving lineage the evolutionary consequences could perhaps develop faster *cf.*[108] than they might do through creeping allelic genetic evolution of inclusive fitness by *W.D. Hamilton’s rule* of kinship selection.

A not unthinkable consequence is that, together with the proposal of homininan mating in very small discrete familial units, several of which were spatially close enough for continual interchange of members and novel information, there was a gradually evolving cognitive trend towards a flexible awareness of alternative behavioural responses, to which an open-ended approach taken by individuals might lead to variable choice depending on how information might be interpreted that was burgeoning and reverberating within and between the tiny social units. Some aspects of the matter demand particular attention, namely, the plausible composition of putative tiny social units, their likely internal, cognitive developmental capacities over each member’s life from birth to death, and the gradual evolution of external relationships, both with neighbours and the natural environment, envisaged with due regard to *time-perspectivism*. From *Australopithecus anamensis* (4.3-3.8 Ma) there elapsed about three-and-a-half million years before the Palaeolithic record (~0.5 Ma) offers evidence that transmission of different techniques or skills hints at the existence of human “cumulative culture”. During that vast span of time there surely were thousands of false-dawns caused by network failures, disappearances of homininan emitters and recipients of information, and reappearances in time or space of various behavioural patterns. Furthermore, as already mentioned, the evolution of adaptive behavioural traits need not be reflected in taxonomically-differentiable biological changes in morphology, ontogeny, physiology, or neurology, such that particular palaeoanthropologically-designated genera or species possessed all, some, or none of the biological adaptations most appropriate for the requisite reproductive success necessary in order for the adaptive zone of *Homo* to become established as the final outcome. The natural selection of homininan adaptations, including bio-behavioural ones, may have been more than just an inexorable goal-directed process defined by inherited allelic reproducibility (*e.g.*, by *Hamilton’s rule* for kinship selection) that was modifiable by some heritable, circumstantially-acquired, learnt responses (*e.g.*, *Baldwin effect*). In contrast to the co-evolutionary *dual-inheritance* (gene-culture) interpretation, a *triple* one is proposed here, because the *differential diachronic (time-wise) evolvability indicated in the homininan fossil record* implies a *third* aspect of the evolutionary mechanism.

This aspect gives pride of place among hominins to the likelihood of increasing exchanges (in contrast to paninans) of accurate *information* between individuals whose corresponding cognitive awareness increasingly made it possible for them to envisage a variety of *alternative neuroethological* behavioural responses. Practising these through trial and error led sometimes to the emergence of heritable *learnt* alternatives which, in turn, could result in actions leading to outcomes that differentially affected the *internal reproductive structures* of different breeding aggregates. Some outcomes were the eventual modification of an aggregate’s allelic genotypical composition. Others were modification, perhaps sometimes less gradual, of an aggregate’s developmental ontogeny, in which a significant part likely was played by evolutionary variations of epigenetic impingements on allelic gene-expression. Nevertheless, neural stem-cell research on chimpanzees and humans indicates that transcriptional enhancers with human-specific activity have affected the evolution of gene targets (conserved from the common ancestor of the two species) in *human accelerated regions (HARs)* that show specific expression patterns of neural progenitor components (notably, outer radial glial cells) in the developing cerebral cortex [109] *cf.*[110]. The human brain embraces a very wide range indeed of *differentially expressed genes* that have cell-type specificity reflected in cellular-level epigenomic features that

suggest their role in the functional specialisation of individual cells [111] [112]. Laboratory research and genomic analysis indicate that the transcriptional enhancer *HAR-123*, present in all therian mammals and demonstrably involved with forebrain-hippocampal connectivity and cognitive flexibility in mice, underwent panin-an-hominin evolutionary divergence reflected in nine nucleotide differences between chimpanzees and humans out of a 442-long sequence [113], which suggests the possibility of the evolution in hominins of a neurobiological increase in cognitive flexibility vis-à-vis paninans during a period of time that could correspond to the Pliocene and Early Pleistocene. Granted that before two-million years ago hominin brains were little bigger than chimpanzee brains today, an intriguing matter concerns when the aforementioned divergence in cerebral cortical evolution might have commenced (maybe during the Pliocene), what precipitating factors, if any, might have initiated it, and what might be an appropriate evolutionary model. A widespread notion is that natural selection of species after the panin-an-hominin divergence produced an increase in hominin brain-size as one “palaeospecies” gave way to the next (*cf.*, “punctuated evolutionary equilibria”). The notion is challenged by the detection of a positive correlation between brain-size and body-mass *within* separate hominin “palaeospecies”. It is a pattern that can arise when individual species undergo increasing trends separately, such that each one shows “*a positive association between relative cranial capacity and time within-species*” [114]. It implies that relative brain-size evolution in the hominin lineage “*seems to be entirely explained by microevolutionary, population-level processes*” [114] albeit “*with an accelerating within-species increase through time... in line with hypotheses that evoke a coevolutionary positive feedback process such as between brain size and sociality, culture, technology, or language*” [114].

A different conclusion is that from dynamical mechanistic modelling with analysis of energy conservation (referrable to uncontroversial biological metabolic and life-history theories) in an “evo-devo” comparison of seven hominin “palaeospecies”, namely, that brain expansion was “*not caused by direct selection for brain size but by its genetic correlation with developmentally late preovulatory ovarian follicles. This correlation is generated over development if individuals experience a challenging ecology and seemingly cumulative culture, among other conditions... the evolution of exceptionally adaptive traits may not be primarily caused by selection for them but by developmental constraints that divert selection*” [115] [117]; this corroborates the notion [118] that human brain size could be an evolutionary “spandrel” *sensu* [119]. “*The absence of direct selection for brain size or skill level in the model contrasts with the longstanding view that human brain expansion was caused by direct selection for increased cognitive ability or behavioural complexity that increases survival, as this is not the case in the model, but such selection may be introduced in the model in the future*” [117]. Whilst not implausible, it is unclear how the evo-devo “spandrel” interpretation could account for the neocortical stem-cell research finding of genetic difference between chimpanzee and humans, nor how their skill levels relate to (let alone correlate with) neocortical neuroplasticity. In a model in which “*skill level is defined as the capacity of an individual to overcome ecological or social challenges to extract energy from their environment and... is measured in information units*” [120], the relative contributions were estimated of genotypical, phenotypical, ontogenetical, ecological, and social interactions, in terms of sensitivity, elasticity, and reactivity, which offer an approach towards a dimensionless appraisal of changes that affected hominin evolution, especially the genus *Homo* whose original genotypical underpinning of phenotypical characteristics played a decreasing part, according to the model, relative to the interplay of the diversity of aspects that moulded the evolutionary trajectory of human ontogeny, cognition, and behaviour. The conclusion from the model is in line with considerations of significant aspects that likely gained prominence, after evolutionary divergence between paninans and hominins, in the particular evolutionary trajectory of human cerebral ontogeny, including cooperative behaviour [121], working memory [122] *cf.* [123], and extensive intracerebral white-matter myelinated neuronal bundles or “tracts” [124] [125].

Perhaps brain research will clarify the part played in the phylogenetic evolution of Hominoidea by the parallel processing of the transmission of information, which is noteworthy in the brain of humans in contrast to macaques and mice [126]. Plausibly, before and during the Pliocene, a very gradual enhancement of parallel processing in hominin brains involved the imperceptible neurobiological evolution of trait-mediated indirect interactions with not only their natural but also their social environments. The Early Pleistocene outcome was a definitive divergence of hominin from panin behaviour. Open to debate is whether or not cerebral parallel processing could be a “spandrel” in hominin evolution. Also open to debate is how far, during the evolution of mammalian ontogenies, impingement of social interaction in addition to, or in response to interaction with natural environments and their affordances, could have affected the neuronal evolution of the noteworthy synaptic differentiation of dendritic spine sizes, each with maybe a storage capacity of 4.1-4.69 bits of information, according to rodent hippocampal research [127] *cf.* [128] For *Homo sapiens* brains, proposals of storage capacity range from 10 TB (terabytes) to 2.5 PB (petabytes); moreover, notwithstanding the widely-cited 86 billion number, the number of human cerebral neurones may be between 62 and 94 billion; 61-73 billion in healthy women; 73-99 billion in healthy men [129].

It may be pertinent to remark that whilst the 10-20 watts (=Joules/second) which power our brain may suffice for a memory storage of barely 4 terabytes (4TB), where 1 byte = 8 binary information digits (bits), the metabolic aspect in relation to conservation of energy becomes complex if cerebral information were to be retained less in binary digital form than in the form of parallel topological definitions (then maybe “All bits are off!”). Of indisputable relevance to the phylogenetic divergence is the comparison of chimpanzee and human cerebral connectomes [125] following the indication of the organisation of neural communities as *network hubs* in human brains [130] by using the analytical methodology of *graph edge-betweenness* [131]. Subsequent research implies that *betweenness centrality of network hubs* in human brains may well not be identical with neuroanatomical modules characterised by domain propensities, but contributes particularly to integrating and modulating information from several hubs [132]. From an evolutionary viewpoint, a provisional interpretation is that a phylogenetic difference between paninans and homininans has led to the organisation of neural communities as *network hubs* in human brains and connecting tracts or bundles of white-matter nerve fibres which continue to form throughout childhood and adolescence. abc

Two relevant matters of interest (cf.[116] [120] [121] [122] [133]) are that (a) the capacity of our young children's working memory soon outstrips, after their age of four or five years, that which has been attained ever by a mature chimpanzee, and (b) throughout long years of childhood and adolescence there continue to develop significant tracts of white-matter bundles of neuronal fibres between different parts of our brain that enhance the facility to remember, plan, and carry out behavioural undertakings by well-documented, contemporary, behaviourally-competent people whose brain is much smaller than most contemporary human brains; for example, Nobel Literature laureate Anatole France's brain (~933 cm³) was only about two-thirds of the size of most people's brains, though roughly similar to the size of brains contained by fossil skulls of *Homo* between two- and one-million years ago whose forebears already had ranged widely throughout the Old World, implying cerebral neurobiological evolution of cognitive abilities far beyond those documented about chimpanzees or bonobos in the wild.

The behavioural versatility of chimpanzees and bonobos in the wild, and the cognitive aptitudes attained by some when in contact with humans, have inspired actualist interpretations of primaeval homininan behaviour. Scholarly attempts to envisage rational scenarios should not be disparaged. Their limitations, however, are obvious in as much as the material record is sparse and ambiguous for the Late Miocene, Pliocene, and first half of the Early Pleistocene. This hampers the development, in human evolutionary studies, of methodologically-useful archaeological and anthropological “middle range” theory cf.[134] of the kind desired by the late-lamented archaeologist Lew Binford [135] who distrusted post hoc ergo propter hoc accommodative argument [136, pp. 194 and 213] and argued in favour of the testing of null hypotheses about aspects of the material archaeological record [137]. Nonetheless, such is the power of arguments which invoke statistical analyses derived from studies, whether in the field or the laboratory, of great-ape behaviour and cognitive ability, that many scholars accept them as providing a suitable lens through which to envisage the behaviour of primaeval homininans. However, what is envisaged could be a mirage. From the standpoint of scientific epistemology and methodology, such *actualist retrodiction* provides but a *weak* explanation of material phenomena because it employs analogical inference that explains them *away*. This can have obstructive consequences, such as the foreclosure of focussing (let alone funding) normative empirical scientific research directed *primarily* towards the material record itself cf.[79]. Nevertheless, it goes without saying that proposals grounded on retrodictive arguments are not necessarily incompatible with the theoretical proposal espoused here that relates the behaviour to *active inference* in accord with the *free energy principle*. The proposal therefore is applicable to the study of behavioural evolution, whether in bonobos, bats, or blackbirds. Its appropriateness is based on consideration of *first principles* in physics which underpin neurobiological mechanisms in sentient Chordata and possibly in other animal phyla. Of particular relevance here is the relationship between the *first principles* and the practical concept of *information* that is employed by physicists and engineers, notwithstanding a gap as yet unclosed between consistent theory on the one hand, and its applicability to biological evolutionary processes on the other. It is to be hoped that suggestions offered here may help towards finding ways to close it, such that in the near future it may be possible to turn rational conjecture into plausible assessment of the likely neurobiological, neuroethological and neuropsychological rates of change that were involved in the late Caenozoic paninan-homininan phylogenetic divergence that has led to significant differences in the social arrangements and social behaviours between the only surviving genera, namely, *Pan* and *Homo*.

It is suggested here that the matters can be approached appropriately by considering (a) the plausible relevance of the concept of the evolution of mammalian brains as *hierarchically mechanistic minds* [83] [84] [85] as neurobiological inference machines that work by *active inference*; (b) the plausibility that there have evolved taxon-specific “*zones of bounded surprisal*” ZBS [80] corresponding to each particular species’ hierarchically mechanistic mind; and (c) the possibility that a particular aspect of very early human evolution involved the transmission of information in and between neighbouring homininan very *small-world* social networks, thereby initiating the differential diachronic (time-wise) evolvability of paninan and homininan hierarchically mechanistic minds that eventually, albeit

extremely gradually, led to a hominin *ZBS* broader than that of chimpanzees and bonobos. In contrast to contemporary humans, chimpanzees have a restricted *ZBS* [79] that thus limits their ability to tolerate large discrepancies between predictions and observations (i.e., to avoid the increase of entropy whenever prediction errors are large), and in particular it constrains their ability to copy, with accuracy and precision, actions that they have seen performed by humans. From the viewpoint of the concept of *hierarchically mechanistic minds*, brains are considered to be hierarchically-organised neurocognitive systems which interact dynamically with their surroundings, such that animals evade surprising or unaccustomed states by their minimisation, through *active inference*, of variational free energy (referrable to the free energy principle of statistical thermodynamics). The interactions involve neural predictive processing and, by maximising marginal likelihood (*cf.*, Bayesian model evidence), they generate perception-action responses of active inference by actively seeking predicted sensory exchanges which can minimise cognitive surprise; such self-organisation can be regarded as self-evidencing. The concept is rooted in the determination by Hermann von Helmholtz (1821-1894) that the work obtainable from a closed thermodynamic system at a constant temperature can be calculated as a thermodynamic potential. In such a “*Helmholtz box*”, the maximum amount of work performed by the thermodynamic process is given by the change in *Helmholtz free energy* and under isothermal conditions its value is minimised when the process reaches equilibrium and hence its final entropy is highest [138]. Helmholtz free energy is measurable as a system’s thermodynamic potential calculated as the internal energy of a system. To complement this thermodynamic formulation of self-organisation to thermodynamic equilibrium, in 1866 Helmholtz, who was both a physicist and a physician, also introduced the concept of “*perception as unconscious inference*” based upon the notion of *minimising a “neuronal” energy* [139] [140]. Variational free energy can be read as a formalisation of Helmholtz’s notion and, his *neuronal energy* in terms of information theory, in line with considerations [141] [142] referrable to Feynman’s noteworthy consideration of quantum physics [143] and Jaynes’ maximum entropy principle [144].

The information theoretic that is *surprisal* (*a.k.a.*, self-information) is regarded, for practical purposes, as equivalent to cognitive *surprise* (or, more simply, to prediction error in predictive-coding accounts of the Bayesian brain). The lesser or greater tolerance of cognitive surprise corresponds, respectively, to a narrower or a broader *zone of bounded surprisal*. *Intolerance* can be interpreted as failing to model or infer the counterfactual outcomes of observed surprising phenomena (including unaccustomed or novel behaviour, whether generated by oneself or others), simply because there was no (evolutionarily-endowed) generative model at hand (or in the head) to predict them (including, of course, an animal’s own unintended accidental behaviour or slip-up: for instance, monkeys often die after falling from trees when they have failed to grasp a high branch to which they had reached out). Plausibly, the experience of cognitive surprise is an outcome of an evolved neurobiological propensity for exploring unorthodox possibilities of available affordances *sensu* [145] [146] that are recognised in an animal’s natural or social environments. The *ZBS* notion contains a temporal memory component because any cognitive surprise is in contrast with the pre-existing unsurprised state of the sentient creature in which surprise is registered. Despite the creature being unconscious or unaware of the pre-existing state, cognitive surprise implies a capacity for a prior state to be challenged, so to speak. The creature’s responsiveness and any resulting neuroethological response involve comparison and contrast with its mnemonic routines. The capacity to do that in hierarchically mechanistic minds is limited by the cerebral neurobiological mechanisms available in different animals, including some within a single taxonomical division, such as the Hominini (hominin) tribe and its Panina (paninan) and Hominina (homininan) subtribal branches which nowadays differ considerably with regard to that capacity.

A few words are in order here about neuroethology, and in particular about what may underlie the receipt of information about a creature’s surroundings (its environment) by its neurones and how they transmit information in response and thereby initiate behaviour (hence the word neuroethology). A rational theory is that a creature’s neuroethological responses depend on its surroundings that themselves undergo continual and continuous change. In line with this view, sentience could derive from an (essentially topological) quantum reference frame that involves a holographic interface (with mathematical attributes of a *Markov blanket** the interior of which is conditionally

***Markov blanket (MB):** “An MB is the set of states that statistically isolates (insulates) internal (systemic) from external (non-systemic) states, such that changes in internal states are mediated by the states of the MB. The MB itself can be partitioned into active and sensory states, which are defined by the following relations: internal states do not influence sensory states, and external states do not influence active states. Now, we should note that the terms ‘active’ and ‘sensory’ are potentially misleading. They are only meant to capture relations of statistical dependence between random variables. This will be crucial to our argument..., as things that we would not readily describe as literally acting or sensing in any meaningful sense can still be captured with this

formalism, since it entails only a statistical enshrouding of systemic states from external ones, and the systematic statistical partition of the whole organism–niche system.” [88 p. 190].

independent of its exterior) on one side of which encrypted external inputs of quantum phase information from the ever-changing environment are registerable for decoding on the other side by internal property-detectors modulated by a mnemonically-informed, temporal comparator. In line with the scale-free space-time background of quantum information theory, quantum reference frames are not only measurement devices but also preparation devices, where *Markov blankets* provide observational contexts (by local reduction of variational free energy at the interface) for neuronal assessments of predictability [147] [148] [149] [150] [151]. Conventional, less far-reaching, holographic interpretations exist regarding neuronal-memory temporality which are consonant with empirical considerations [152] [153].

A creature’s *ZBS* delimits its capacity to respond to unpredictable phenomena when they occur. These may be part and parcel of widespread, naturally-evolving change in the landscape background, and also, in addition, impingement in the foreground by other creatures (including humans), for whom these particular additional modifications of their common surroundings can have (“cultural”) deontic value that may be communicated between individuals. It has been suggested that, in humans, “*cooperative communication*” could be the result of “*an evolved adaptive prior belief that their mental states are aligned with, or similar to, those of conspecifics*” prioritising behaviours that “*minimize uncertainty and optimize an individual’s internal model of the world... allowing for the development of a shared narrative that is used to disambiguate interactants’ (hidden and inferred) mental states. Thus, by using cooperative communication, individuals effectively attune to a hermeneutic niche composed, in part, of others’ mental states; and, reciprocally, attune the niche to their own ends via epistemic niche construction. This means that niche construction enables features of the niche to encode precise, reliable cues about the deontic or shared value of certain action policies (e.g., the utility of using communicative constructions to disambiguate mental states, given expectations about shared prior beliefs). In turn, the alignment of mental states (prior beliefs) enables the emergence of a novel, contextualizing scale of cultural dynamics that encompasses the actions and mental states of the ensemble of interactants and their shared environment*” [103].

In neuroethological synergic contexts, the biological concepts of stigmergic behaviour and sematectonic communication have long been recognised as helpful. We are thereby forcefully reminded that co-existence with our surroundings is no less a two-way affair for humans than it is for ants, frogs, cuckoos, or rabbits. Their environments impinge on them no less than those sentient creatures impinge on their surroundings, be these physical, natural, or social. Mobile sentient creatures tend to respond to their environments with specific niche-constructions. Even among the very versatile Primates, humans are distinctive in carrying out a remarkably wide and varied range of niche-constructions that often are socio-culturally differentiable. To aspects of these, moreover, we are able to assign mnemonic signifiers that we can communicate or transmit selectively in ways that are particularly flexible and efficient (notably, spoken language) with regard to trying to achieve appropriate rapid outcomes. Most of us have learnt (often to our cost) that outcomes are easier to envisage, and subsequently to recognise, than were our motives and underlying motivation. This is so, whether the outcome is playfulness, obtaining food or drink, making this or that object, speaking or singing, walking or dancing, doodling or sculpting. The mistakes we make notwithstanding, it is the exceptional human capacity to draw on the different varieties of memory retained in our brains (short-term working memory and long-term working memory, procedural memory, semantic memory, episodic memory, and prospective memory) which enables our hierarchical mechanistic minds to work as self-evidencing, neurobiological inference machines. Plausibility has grown in recent years that the underlying generative process is dependent on neuronal predictive processing and consequent updating of Bayesian model evidence referable to neuronally-registered Bayesian priors [88] [154] [155] [156], following research at the close of the 20th century which showed the neurophysiological significance of neuronal predictive processing [157]. It is important to stress that it is our *embodied activity of enactment* which realises any generative model whatsoever that may have been formed by priors about what our surroundings could have led us to expect or anticipate. In other words, *active inference* is about *acting* (reacting) and *not* about readjusting or *re-presenting* a model (representing it “mentally”); thus, more than merely in some disembodied cerebral hierarchical mind, the reference of the generative model is in respect of the neurobiological work undertaken physically by a brain’s hierarchically mechanistic mind.

The foregoing paragraphs highlight the matter that the development of our modern human brain’s complex consciousness, characterised by widespread attention-sharing and communal reflexion about alternative policies, is a matter that has to have been, without doubt, a drawn-out biological process. It involved aspects of genetics which enhanced gene-culture evolution (e.g., *human accelerated regions HARs*, and epigenetic impingements on gene-expression), and no doubt produced some demographically-skewed reproductively-effective communities in which

learnt transmission of behaviour played a part. Any or all of those aspects will have influenced human ontogenetic evolution, though, most likely, the corresponding neurobiological evolutionary changes were imperceptibly gradual. It should be borne in mind that, separated within the skull from the world beyond, our brain houses between 60 and 100 billion neurones, many of which have hundreds or even thousands of synapses with others, so that interchange of each with its surrounding cells affects outcomes of active inference and consequent exchange with the surrounding neighbourhood of our body and the bodies of our fellow creatures. Our brain is a scaled-up Primate brain, remarkable perhaps, albeit not extraordinary [158]. What *is* extraordinary, however, is that what evolved in our ancestral phylogenetic lineage has had the unique outcome of a communicative fluency that has evolved in us (but not in great apes, or any other creature) which is demonstrated by spoken language that enables (or, at the very least, enhances) the transmission of information about *alternative* interpretations of our perceptions about what is happening around us and of *alternative* interpretations of courses of action that are open to us; this *open-ended* [159] approach to behavioural *alternatives* seems to be a uniquely human trait in hierarchically mechanistic minds that derives from *how information is deployed*.

3. Information and hominin *small worlds*

It is not unthinkable that, from the Late Miocene onwards, the *transmission of information* in and between neighbouring hominin very *small-world* networks affected *differential evolvability* within the hominin Hominini tribe of the hominin Hominina subtribe vis-à-vis the panin Panina subtribe. A plausible evolutionary conjecture is that during the period between ~7.5 and ~3.5 Ma hominin behaviour evolved through the very slowly-increasing versatility of tiny, contiguous, familial units of rarely above a dozen members present together at any given time, whose reciprocal exchange of kin of both sexes produced mixed-sex philopatry in social units, very often including an alloparental individual (predominantly under thirty years old), which co-existed and evolved in mosaic landscapes. Whatever may have been the social arrangements of paninans during the Late Miocene and Pliocene, it is not unreasonable to imagine, contrary to some rational arguments [63] [64], that they may have been unlike those contemporary chimpanzees or bonobos which nowadays have multifemale-multimale troops. Whether or not primaeval panin or primaeval hominin social units in the Late Miocene were as small as those of contemporary gorillas today *cf.* [160], they likely never contained more than a dozen individuals. The emergence in humans of *large* multifemale-multimale stable social units (*e.g.*, *bands*) may have been a *late* evolutionary development, perhaps only in Late Pleistocene *Homo* and associated with wide-ranging ecological dominance enabled by a capacity to consider and carry out alternative plans [161] envisageable by virtue of an expanding *zone of bounded surprisal* that had far outstripped that of paninans. Conflict between contiguous social units may have been a very much later tendency, maybe absent before the Middle Pleistocene, in response, perhaps, to depletion of local environmental resources from causes ranging from increase in local densities of hominin populations to scarcity of locally-available bioenergetic resources on account of floods, wild-fires, droughts, plagues of pests, competition by other creatures, increase of predators, earthquakes, volcanic eruptions, or disruptive secular climatic change.

In contrast to a widespread presumption by anthropologists that hostility between chimpanzee troops were to have been, *ipso facto*, a foundational component of hominin social units, it is proposed that an evolving broadening of hominin *zones of bounded surprisal* (ZBS) enabled a greater tolerance of neighbours. This implies the plausibility that, through *active inference* under the *free energy principle*, there likely began to evolve neurobiological cerebral dispositions, probably in *Australopithecus*, which fostered *coordination* within social units and *cooperation* of their component members, and the eventual consequence of *coordination*, *cooperation*, and *collaboration* with neighbouring social units. It is important to distinguish between the 3 "co-" words, because they are not synonyms. Coordination of anything ensures that its constituents or components are functionally in harmonious relationship (*e.g.*, they may be people as in an army, or cogs as in a machine). Cooperation *on* anything involves working together (joint action) *with* somebody *on* something. Collaboration *about* something involves working together (joint action) *with* somebody *towards* achieving a goal or particular outcome or aim. Note the different prepositions, and the different placing of "anything" and "something"; also note that cooperation is about *working effortfully*, whereas collaboration is about *potential achievement* where the exchange of relevant information is fundamental. The apogee of human *cooperative communication* was the outcome of a drawn-out, uneven development that probably came to fruition in *Homo* during the Pleistocene, enhanced eventually by spoken language (involving exchange of information by symbolic reference and an ability to rearrange referable items stored in memory which far exceeds the ability of great apes). As already quoted above, "*cooperative communication*" between individuals could be the result of "*an evolved adaptive prior belief that their mental states are aligned with, or similar to, those of conspecifics*" prioritising behaviours that "*minimize uncertainty and optimize an individual's internal model of the world... allowing for the development of a shared narrative that is used to disambiguate interactants' (hidden and inferred) mental states*" [103].

If the onset of the expanded hominin *ZBS* were to have been indeed in the Pliocene genus *Australopithecus*, it behoves us to conjecture a reasonable scenario of social arrangements. In contrast to panin social arrangements, they should fulfil the criterion of enhancing the recognition of, and the coordinated response to information that is imparted. These are attainable more rapidly, more accurately, and more appropriately in the absence of the hustle and bustle of a noisy or rowdy troop in which customary behaviour crowds out or stifles unaccustomed individual responses which, so to speak, get nipped in the bud. By contrast, continual social intercourse, within and between very small, agile, neighbourly units that are related by kin, fosters the expeditious use of novel information. Within hominin units, paternal involvement in a very *small* social unit likely enhanced the transmission of information between members, thereby heightening versatile awareness, from infancy onwards, about alternative policies, strategies or flexible tactics which may be available in situational contexts that provoke less cognitive surprise in duly-prepared hominins than in ill-prepared panins. Such involvement does not imply paternal concern for young offspring; there are indeed contemporary societies, including some hunter-gatherers, in which fathers do not pay particular attention to their young children. Considered from a neuroethological standpoint, it is plausible that the exposure of toddlers to the several respective behaviours performed by individuals of *all* ages who were close female *and* male kin, came to influence, imperceptibly by *active inference*, the gradual development, during several million years of hominin evolution, of the behavioural *variability*, carried out by other members of their very small tightly-knit social units, that was - and is - observed closely by toddlers. It is an evolutionary development that has resulted in a broader human *ZBS* than that of great apes. It enables our extraordinarily wide range of personal behaviour, including attempts to copy faithfully (*i.e.*, with accuracy and precision) some behaviours of other individuals or to explore, in open-ended fashion, unanticipated novel or surprising aspects of self-generated behavioural "accidents" ("Eureka!", "Aha!" moments).

Nevertheless, almost all of these are ephemeral. Very, very few ever became transmitted such as to be recognisable in the Pleistocene record as instigators of widespread heritable behavioural traits (*a.k.a.*, "cumulative culture"). Very *small-world* behaviours are as much subject to punctuated evolution as are biological species. Drawing on active inference, and paying due regard to time-perspectivism, "bottom-up" considerations highlight the pitfalls to transmission [48]. A formal interpretation, "top-down", is that social biases against non-conformity impede recognition of useful possibilities [162]. Collapses of hominin populations, inferred from evident punctuated evolutionary palaeogenetic bottlenecks (*e.g.*, in the genus *Homo* cf. [163] [164]; perhaps leading to the disappearance of *Homo floresiensis*, *H. naledi*, *H. luzonensis*, "Denisovans", and maybe Neanderthals) could have reduced the widespread availability of, or accessibility to useful possibilities, though if occasionally these were available and accessible a survivor might have grasped and developed them.

The external dynamics of a relationship between one social unit and another, are not independent of the internal dynamics of each, that, in turn, depend on the developing internal dynamics of each constituent adult or growing child. Behaviour at any one of these three levels may inform behaviour at any other, particularly so within and between "*small-world*" social units of around a dozen members each. Perhaps a word more appropriate than "levels" is "windows", by analogy with 3 windows that are open together, all at the same time on my computer screen throughout an interactively evolving 3-person video chat. It may not be far-fetched to regard each level (or open window) as containing elements that perhaps are functionally analogous to those biological ones, within any organism and its constituent living cells, which may be regarded as network "motifs" defined by feed-forward and feed-back controls that are genetically or epigenetically influenced by transcription factors [165]. In terms of graphical network analysis, such "motifs" correspond to subgraphs. Plausibly, the internal dynamics of a social unit impinged *externally* on the evolvability of neighbouring social units that, together with it, made up a broad spatiotemporal network which, as long as other things were equal, approximated to a power-law distribution of the node-degrees. Likewise, within each social unit, the dynamics of the behavioural impingements of its constituent adults and children continually affected the evolving network formed by them *within* their social unit. Moreover, impingements by their own within-body network of interacting physiological and other internal systems and experiences affected *its own* life-long evolution. The temporal scales or rates of evolvability of the three "windows" must be distinguished. A particular matter of interest involves the transactional *asynchronicity* of reciprocal collaborative behaviour between individuals (*e.g.*, "I'll help you this time; you'll help me next time"): conscious awareness and memory of it characterise human relations and reputations both within and between social units. The matter has been considered recently [166] [167] from a perspective of statistical physics which combines a version of the Lenz-Ising model of physical phase transitions with Markov chain Monte Carlo random sampling (*e.g.*, Metropolis-Hastings algorithm) where it is not possible to carry out direct sampling of a probability distribution. Perhaps this approach could offer a way to elucidate and model the Plio-Pleistocene hominin behavioural evolutionary divergence from panin behaviour.

Obvious evolutionary limitations that can impede transmission of behaviour (such as skills) within and between each of the aforementioned three dynamical levels, or open windows, are imposed by spatial expansion or temporal

extension, either of which can eradicate interconnectivity or power-law approximation, or both [168] [169]. Perhaps theoretical aspects of this problem, with regard to the evolution of early hominin behaviour, could well be treated in the future from the graphical network standpoints of *edge-betweenness* and *node-betweenness* [132]. Computational physicist Mark Newman [124, p. 173] wrote, “*It seems plausible that nodes with high betweenness centrality could have influence within a network, by virtue of their control over information passing between others... The nodes with highest betweenness are also the ones whose removal from the network will most disrupt communications between other nodes...*” Redundancy of the information transferred seems to protect against disruption [170]. Modelling Early Pleistocene human behaviour and its technical products could be attempted perhaps along the lines of Newman’s percolation algorithm [124, pp. 595-599]. The matter of *adaptive zones* (fitness landscapes) could well be pertinent, and probably the ZBS notion is relevant at both internal and external levels of behaviour of each very *small-world* social unit. A scale-free approach, if possible, might be capable of embracing modularly evolving outcomes *cf.* [171] that are commensurate with *time-perspectivism*, though, at best, reconstructing the gradual evolution of a complex system can provide no more than plausible models for interpreting human evolution and early Palaeolithic behaviour. The difficulty to be overcome is that of how to link network properties, such as centrality, redundancy, percolation, and asynchronicity, with the informational dynamics of the transmissibility of the endurance of behavioural innovation and skills in the face of unforeseeable constraints or hazards (*e.g.*, population collapse, *etc.*) when viewed through the lens of time-perspectivism. Investigation could involve recourse to hypergraph modelling (*cf.*, [172] [173] of plausibly feasible ways by which very small-world social units of primaeval hominins likely evolved differentially in evolving spatiotemporal circumstances between ~7.5 and ~1.3 Ma, whereafter *Homo* was the sole remaining genus.

The suggestion put forward here is that over the course of three or four million years, during the Pliocene and well into the Early Pleistocene, hominin behaviour, evolved through the slowly increasing versatility of tiny, contiguous, familial social units, each containing rarely more than a dozen members present together at any given time, whose reciprocal exchange of kin of both sexes produced mixed-sex philopatry (*syn.*, “bisexual” philopatry) in social units, very often including alloparental members (almost all under thirty years old), which co-existed and evolved in mosaic landscapes by the creation of contiguous neighbouring units by budding, plausibly within a two- or three-hour walk away. The composition of contemporaneous panin units in woodland environments may have foreshadowed their present configuration, though possibly the dearth of fossil remains might suggest that troops could have been smaller than nowadays. Be that as it may, the proposal here is that the phylogenetic split between paninans and hominins was between multifemale-multimale paninan social units (troop or mobs) with male philopatry, and small hominin units characterised by mixed-sex philopatry comprising nuclear family units under stable *biparental* care, with close paternal proximity to infants and children as well as their maternal care, from which there was *mixed-sex dispersal* that enabled the colonisation of new localities and possible expansion of *mixed-sex philopatry in neolocalities nearby*.

With regard to behavioural heritability, stable biparental care influences not only *intragenerational* relationships but also *intergenerational* hereditary demographic structures: thus Gendron et al. wrote [174, pp. 188-190] “*...the process of regulating a body’s internal systems, called allostasis..., drives the bidirectional relationship between the brain as a generator of culture (in concert with other brains) and a product of culture... humans are social animals because we assist one another with the necessary physiological regulation to meet the changing demands of the physical and social environment – that is, humans help one another to establish and maintain allostasis... (which) is supported by the physiological dependencies that arise during early social contact... ... humans’ extended period of physiological dependency on caregivers provides the necessary conditions for infant brains to wire themselves to their physical and social surroundings. As the infant brain bootstraps a set of experiences into its wiring, it develops a model for how to best regulate its body in a given set of contexts (i.e., within the constraints of their culturally shaped world). The “outside” conditions of this world offer affordances or “possibilities for action” that establish and maintain the brain’s internal model, which is inherently culture-dependent... ... one brain’s internal model guides behavior, which creates a set of affordances that impact others’ allostasis, shaping their behavior and experiences in turn. Eventually, allostatic regulation shifts away from primary caregiving relationships, which are supplanted by self-regulation based on a set of learned concepts that are continually reinforced by the social structuring of the environment. This social dependency across the lifespan further ensures the transmission of culture across generations.*”

The creation of neighbouring contiguous social units by budding, and thus related by kin, permitted neighbourly cooperation and even collaboration in activities such as obtaining and sharing bioenergetic resources whenever local environmental circumstances or constraints may have led to exchange of information about what, where, and when a resource might be available that could be shared appropriately. It is plausible to regard as fundamental the cooperative transmission of both the prerequisite information about aims like those, and the feasible collaborative means to achieve them. The “*small-world*” concept [175] [176] is suitable for theoretical network analysis [177] which is appropriate for

modelling the transmission of information among continually budding cells of an evolving network [177] such as the postulated very small social units of primaeval hominins. Against the existential fragility of such small units, very, very many of which undoubtedly succumbed to extinction within a few generations, there must be weighed a plausible counterpoise of greater or faster development of information gleaned by each in their respective contiguous geographical areas about the availability of bioenergetic resources necessary for survival and reproduction. This information determines the *fitness* of a social unit, where *fitness* here can be understood as in *Bianconi-Barabási* model networks [177 Chapter 6] [178]. As budding of units increases, complications develop on account of not only the randomness and vagaries of the budding process, but also the exchange of information between nodes of the network of buds. A well-studied aspect of network topology is that of how the dynamics of scale-free distributions of nodes (*i.e.*, vertices in graph topology) can produce complexity, likened often to abrupt phase transitions in statistical physics and chemistry, *e.g.*, ice↔water↔steam, *cf.*[177 Chapter 3]). Perhaps whenever new accrued knowledge became overwhelmingly present in a very small hominin social unit, the experience was “phase-like” in as much as there may have taken place an abrupt transition to a shared state of awareness of what had accrued, with corresponding behavioural modifications. Nevertheless, it may well be that only after the emergence of the genus *Homo* was there an evolutionary trend towards loosening the shackles of routine custom defined by inherited (“instinctive”) ethological responses.

An interesting possibility is that transitional acceleration might have been involved not only in the original Early Pleistocene behavioural distinctiveness of the genus *Homo*, but also in subsequent (perhaps Middle Pleistocene) developments in cooperative communication and communicative fluency (*e.g.*, using spoken language with symbolic referents) and so-called “cumulative” technological culture. Be that as it may, it could be worthwhile for network scientists to collaborate with those physicists and mathematicians who are involved with the formal analysis of active inference under the free energy principle, as well as with mathematicians interested in evolutionary processes or biological transitions, in order to consider the possibility of developing formal models that could link their respective interests, with a view to investigating models of complex systems that might offer alternatives to be held up against palaeoanthropological and Palaeolithic evidence, in order to suggest accounts that others might consider plausible of the evolution - biological, social, psychological, cultural - from the Late Miocene to the 21st century BCE, of “*Homo informatio*”.

There undoubtedly was an ever-present vulnerability of very *small-world* social units to mishaps or misfortune. There were existential threats to the reproductive success of very small, agile, fragile, social units. It is likely that they resulted in many false dawns, and underlie the imperceptibly slow, gradual evolution of the hominin clade, including the evolution of and *within* the genus *Homo*, not only its morphology, but also its cognitive and technical aptitudes (*cf.* [48]), shielded, according to the proposal offered here, by the advantage over paninans that was conferrable by a greater facility in the exchange between small neighbouring kin-related familial units of information appropriate for maintaining network fitness in a wider diversity of environments than the woodland habitats of paninan mobs. Plausibly, very many hominin units were extinguished because of unforeseeable circumstances. Exchange of information diminished or ceased between very *small-world* units that became widely separated by distance from other units, and often isolated. It is therefore unsurprising that assemblages of core-and-flake artefacts continued to be the sole handiwork at some Palaeolithic sites when at others bifacial preparation of hand-axes was taking place. Prehistoric archaeologists and ethnographers are accustomed to documenting noteworthy differences in the behavioural or technological complexity of people who lived at the same time but in different places. Their extinction doubtless expunged from the fossil record many “palaeospecies” of hominin genera, including “palaeospecies” of the genus *Homo*. They could have ranged from unanticipated deaths, illnesses, maladaptive genetic inheritance, or the preponderance in a very small social unit of either boys or girls, to unpredictable external impingements of climate, predators, or sporadic uncooperative or uncollaborative hominins with ensuing friction or interpersonal conflict, and here a statistical possibility of personal non-cooperation or non-collaboration by an individual is compatible with considerations about active inference under the free energy principle, which indicate that a lone individual could refuse to accept change and establish a social unit that maintained previous behaviour [179]. Such idiosyncratic responses may underlie the coetaneous existence of anachronistic archaeological assemblages or asynchronous aspects. Just as with other organisms, stochastic processes affected the evolution of our human ancestors and their behaviour [48].

4. Concluding Remarks

The suggestion proposed above is that the different ecological surroundings that had been evolving from Late Miocene times impinged differently on the last common ancestor of woodland-dwelling paninans and mosaic-landscape-dwelling hominins. The former evolved into present-day troops with male philopatry where promiscuous males are unable to identify their own offspring and unable to differentiate these from those of other males, hence, without close paternal proximity, it is the mothers alone who know and rear their offspring and from whom the offspring receive most

of their information during the time when their brains are growing. Field research indicates that chimpanzee females on reaching menarche do not become pregnant by mature sexually-active males in their natal troop and encounter sexual partners in other troops, whereas sexually-active young males do not seek females in other troops whose males are hostile anyway to alien males. The hierarchical structures of paninan troops reinforce customary routine behaviours that crowd out the appreciation of idiosyncratic behaviour, let alone any transmissibility of information related to it. Their members' *zone of bounded surprisal* is less tolerant of novelty than is that of modern humans. It goes without saying that, by natural selection, paninan evolution has involved specific adaptations to woodland-living with enough available fruit and other foodstuff to enable reproductive success and intergenerational continuity.

It is suggested that, by four-million years ago, sparser mosaic-landscapes were affording less food-security to hominins (e.g., *Australopithecus anamensis*), whose existential reproductive success (adaptive, Darwinian fitness) was to depend on the efficient transmissibility of information about what was available where, and when, and how to proceed to get it, including about whom it should fall upon to help to do so, all of which led very gradually to evolutionary adaptations, which included a broadening of their *zone of bounded surprisal* and hence their greater tolerance to unorthodox exploitative policies, strategies, and tactics. These, in tightly-knit families, are imbibed by infants and young children whose fathers' behaviour together with that of all other older individuals in close proximity, is responsible for as much transmission of information as is their mothers' attention to them. However, the flip side, so to speak, is that fathers must be there for them in order to be watched by them. Hence fathers, by their presence, can become aware that they have particular ties with their offspring. This *became possible* in *small* hominin social units with *mixed-sex philopatry* which out of *necessity* could not be other than *small* where bioenergetic resources were sparse locally. Rarely could large social units of hominins be sustainable in mosaic landscapes wherein the amount of edible stuff was scanty that was forageable or scavengeable within a spatial radius of movement possible for a small cohesive social unit while maintaining its balance of energy (i.e. intake of calories *versus* output of energy expended in order to get them). Active inference underpins existential success that in human cognition is characterised by "5 E's", being embedded, embodied, enacted, extended, and *evolved*.

Hominin evolution since 7.5 Ma has been an unimaginably slow, long drawn-out, process. Undeniably, small social units can have reproductive success only if heterozygosity is maintained. This requires outbreeding. It is not unthinkable that primaeval hominins practised *mixed-sex philopatry* and *mixed-sex dispersal* of sexually-active members enabling thereby the establishment of neighbouring kinship-related small social units, between which there was exchange of kin, thus maintaining heterozygosity *and* the fluid social relationships (unlike the hostility between neighbouring chimpanzee troops), including expedient cooperation or collaboration. From the standpoint of the inherited evolutionary aspects and the integrated or extended evolutionary synthesis, it is conceivable that both *Hamilton's rule* about inclusive kinship and (perhaps especially) the *Baldwin effect* whereby transmissibility of information and behaviour perhaps may skew reproductive success within and between the social units of a species, fostered the survival, reproductive success, and evolution of hominins.

The proposal outlined above need not imply that burgeoning *accrued knowledge* reflects somehow a new biological evolutionary transition [180] *cf.* [181] [182], though, were it to be doing so, a transitional phase could be of very long duration and incomplete at present, when consideration is taken into account of various kinds of ecological transitions that have been analysed [183]. Putting the focus on Pliocene primaeval hominins, incipient "*Homo informatio*" began to have a physical shape less like that of a chimpanzee and more like that of obligate bipedal human beings whilst exhibiting behaviour hardly recognisable as human from any viewpoint whatsoever that takes as its referents human behaviour that has been observed or documented, or even, by possible analogy, inferred from the interpretation of archaeological remains from the Holocene or Late (Upper) Pleistocene. The four-million-year-long, evolutionary transformation to behaviourally-"modern" "*Homo informatio*" human beings from Pliocene hominins, whose behaviour we would be barely able to recognise as remotely human should we have been able to observe them, has been an imperceptibly slow, long drawn-out, transitional process. It must be viewed without hubris and with time-perspectivism. Salutary minimalist advice was given fifty years ago by the late-lamented Glynn Isaac in a timeless essay [184] that is as relevant to anthropologists today as it was when Glynn penned it in 1974. Read it!

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- [5] Wikipedia, (2024), <https://en.wikipedia.org/wiki/Primate>; and Wikipedia, (2024), https://en.wikipedia.org/wiki/Human_evolution. Please take note that the word *hominin*, as used here, includes not only *homininans* (today's humans and fossil precursorial humans) but also *paninans* (chimpanzees and bonobos); which is why *homininan* (rather than *hominin*) is the word that is preferred here which exclusively refers to *Australopithecus*, *Paranthropus*, *Kenyanthropus* and extinct skeletal forms of *Homo*. There are alternative classificatory arrangements within the Hominidae that vary according to interpretations of inferences drawn from genetics and comparative morphology. Readers unfamiliar with Biology should bear in mind that family, genus, and species, are fundamental and obligatory defined categories of formal zoological taxonomy (though their names themselves can be changed), whereas superfamily, subfamily, subgenus, subspecies, tribe, and subtribe, are optionally definable categories to which variable content can be assigned according to differently-chosen criteria that are often the object of dispute, especially in palaeontology. In order to side-step wrangles, the neologism “palaeospecies” is suitable wherever the context does not require Latin identification of particular Pliocene or Early Pleistocene homininan genera or species.
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N.B., The published version contains numerous errors, the most egregious is on p. 263 where “ $x=p=a=m$ and that $y=q=b=n$ ” appears in place of the submitted manuscript’s “ $x\neq p\neq a\neq m$ and that $y\neq q\neq b\neq n$ ”, and among other egregious departures from the manuscript are “worked” for “word” on p. 262, and “con-linear” for “non-linear” on p. 264: all the many errors owe to the journal's editor informing the authors that, on account of a personal editorial logistical inconvenience, proofs would be corrected by the editor himself and would not be sent to the authors who thus were denied any possibility of contrasting their manuscript with what the editor arranged, or rather *re-arranged*, to be published.
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Table 1: A Possible Self-Reproducing Very Small-World Social Unit

Table 1: A Possible Self-Reproducing Very Small-World Social Unit A possible 15-year-long developing membership of a nuclear family is shown, elaborated from the creation of the first pregnancy by its founding partners of U_{10} to the final year of their life when they are 25 years old and there are 10 members. A more plausible scenario is one where U_{10} consists of a reproductive-age male with <i>two</i> female partners of reproductive-age (and maybe another reproductive-age male with none). Even if one baby was born every year, the likelihood of infants/children dying before reaching adulthood renders it plausible that at any one time such a U_{10} would not have consisted of 20 members; perhaps rarely more than 15+ and plausibly not more than a dozen being together at any one moment in time. The situation thus envisaged need not imply a theory of emigration by only post-menarcheal female offspring (<i>i.e.</i> , from units notionally of <i>male</i> philopatric characteristics), were there also to have existed mixed-sex philopatry and mixed-sex emigrations that founded neolocalities, at some of which mixed-sex philopatry could have been perpetuated; furthermore, because brother-sister incest probably no more characterised primordial humans than it does modern chimpanzees, one U_{10} member likely was a reproductive-age emigrant from some notional neighbouring social unit “V”, not shown in Table 1 but who would lend plausibility to a suitably-modified Table 1 that included such an individual. Reproductive continuity is possible within small family units in which few surviving newborn members survive beyond the age of 25 years, as indeed has been the case many in communities lacking adequate sanitary or health care in recent centuries.				
Sequence of increase by births in a monogamous family unit (U_{10}, U_{11}, U_{12},...) up to the possible formation from it of a new monogamous family unit from U_{11}, which offers the (albeit incestuous) repetition of the U_{10} situation. Size of unit membership in brackets ($n=$). It is assumed there are no twin or triplet births.	Unit membership: birth partners(m,f) together with male(m) and female(f) offspring added in order of birth (years of age in brackets). It is assumed there are never miscarriages, still-births, or infant, child, or adolescent mortality, and that U_{10} partners survive until t_8 . Notes: (1) by “ $\geq 11/\leq 12$ ” is meant that at the time of fertilisation of the ovum a partner is not older than 12 years of age and not younger than 11 years of age; (2) by “ ≤ 1 ” is denoted the age of a baby born after 8 months in utero but not yet one year old (age 0 <i>i.e.</i> ≤ 1).	Times, t, in years from each fertilisation of an ovum with ensuing pregnancy. It is assumed 2 years elapses between each fertilisation that has caused a pregnancy that went to term.	Offspring and sex at times (years) t_0, t_1, t_2, \dots	Ages in years of family members at time t. (m=male; f=female) It is assumed that births of boys and girls alternate. The order shown is where a boy is born first (the order can be inverted, of course). Note: It is assumed that before the second pregnancy begins with fertilisation of its ovum, there has to have elapsed 2 years (t_0-t_1, t_2) from the fertilisation of the ovum that began their first pregnancy, corresponding to 8 months of pregnancy+14 months of lactation, throughout which 2 years it is assumed that fertilisation of other ova does not happen.
$U_{10}(n=2)$	1m($\geq 11/\leq 12$); 1f($\geq 11/\leq 12$)	$t_0 = 0$	0	($\geq 11/\leq 12$)m; ($\geq 11/\leq 12$)f
$U_{11}(n=3)$	1m(12); 1f(12); 1m(0, <i>i.e.</i> ≤ 1)	$t_1 = (t_0+1)$	1m	12m; 12f; 0(<i>i.e.</i> ≤ 1)m
$U_{12}(n=3)$	1m(13); 1f(13); 1m(1)	$t_2 = (t_0+2)$	1m	13m; 13f; 1m;
$U_{13}(n=4)$	1m(14); 1f(14); 1m(2); 1f(0, <i>i.e.</i> ≤ 1)	$t_3 = (t_0+3)$	1m; 1f	14m; 14f; 2m; 0(<i>i.e.</i> ≤ 1)f (see Note above)
$U_{14}(n=5)$	1m(15); 1f(15); 1m(3); 1f(1); 1m(0, <i>i.e.</i> ≤ 1)	$t_4 = (t_0+5)$	1m; 1f; 1m	15m; 15f; 3m; 1f; 0(<i>i.e.</i> ≤ 1)m
$U_{15}(n=6)$	1m(17); 1f(17); 1m(5); 1f(3); 1m(1); 1f(0, <i>i.e.</i> ≤ 1)	$t_4 = (t_0+7)$	1m; 1f; 1m, 1f	17m; 17f; 5m; 3f; 1m; 0(<i>i.e.</i> ≤ 1)f
$U_{16}(n=7)$	1m(19); 1f(19); 1m(7); 1f(5); 1m(3); 1f(1); 1m(0, <i>i.e.</i> ≤ 1)	$t_5 = (t_0+9)$	1m; 1f; 1m, 1f, 1m	19m; 19f; 7m; 5f; 3m; 1f; 0(<i>i.e.</i> ≤ 1)m
$U_{17}(n=8)$	1m(21); 1f(21); 1m(9); 1f(7); 1m(5); 1f(3); 1m(1); 1f(0, <i>i.e.</i> ≤ 1)	$t_6 = (t_0+11)$	1m; 1f; 1m, 1f, 1m, 1f	21m; 21f; 9m; 7f; 5m; 3f; 1m; 0(<i>i.e.</i> ≤ 1)f
$U_{18}(n=9)$	1m(23); 1f(23); 1m(11); 1f(9); 1m(7); 1f(5); 1m(3); 1f(1); 1m(0, <i>i.e.</i> ≤ 1)	$t_7 = (t_0+13)$	1m; 1f; 1m, 1f, 1m, 1f, 1m	23m; 23f; 11m; 9f; 7m; 5f; 3m; 1f; 0(<i>i.e.</i> ≤ 1)m
$U_{19}(n=10)$	1m(25); 1f(25); 1m(13); 1f(11); 1m(9); 1f(7); 1m(5); 1f(3); 1m(1); 1f(0, <i>i.e.</i> ≤ 1)	$t_8 = (t_0+15)$	1m; 1f; 1m, 1f, 1m, 1f, 1m, 1f	25m; 25f; 13m; 11f; 9m; 7f; 5m; 3f; 1m; 0(<i>i.e.</i> ≤ 1)f