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Four reasons for scepticism about a human major transition in social individuality

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The 'major transitions in evolution' are mainly about the rise of hierarchy, new individuals arising at ever higher levels of nestedness, in particular the eukaryotic cell arising from prokaryotes, multicellular individuals from solitary protists and individuated societies from multicellular individuals. Some lists include human societies as a major transition, but based on a comparison with the non-human transitions, there are reasons for scepticism. (i) The foundation of the major transitions is hierarchy, but the cross-cutting interactions in human societies undermine hierarchical structure. (ii) Natural selection operates in three modes—stability, growth and reproductive success—and only the third produces the complex adaptations seen in fully individuated higher levels. But human societies probably evolve mainly in the stability and growth modes. (iii) Highly individuated entities are marked by division of labour and commitment to morphological differentiation, but in humans differentiation is mostly behavioural and mostly reversible. (iv) As higher-level individuals arise, selection drains complexity, drains parts, from lower-level individuals. But there is little evidence of a drain in humans. In sum, a comparison with the other transitions gives reasons to doubt that human social individuation has proceeded very far, or if it has, to doubt that it is a transition of the same sort.

This article is part of the theme issue 'Human socio-cultural evolution in light of evolutionary transitions'.

1. Introduction

The 'major transitions in evolution' are mainly about the rise of hierarchy, the advent of new individuals at ever higher levels of nestedness, with ever greater hierarchical depth, over the history of life. They are about the origin of the eukaryotic cell from prokaryotes, multicellular individuals from free-living protists and highly individuated colonies or societies from solitary multicellular individuals [1–4]. Some would include human societies, either as an instance of a transition to the colony level or as a level that is somehow above the colony level. But there are reasons for scepticism, reasons to doubt whether we deserve to share even the colony level with such socially accomplished superorganisms as ant and bryozoan colonies.

Here I offer four reasons for scepticism about a human major transition. The point will not be to deny that humans are special creatures, replete with marvelous adaptations. Indeed there is something extraordinary about the generality of our adaptations, capable as we are of responding rapidly to a vast and disparate array of challenges. Culture is surely part of that but also individual behavioural flexibility and responsiveness in real time to successes and failures [5]. But the question here is whether these extraordinary adaptations add to our individuality at the colony level. Marvellousness of adaptation, even social adaptation, is one thing, and individuality at the social level is another.

The purpose of this paper is to raise doubts, doubts that arise from a macro-evolutionary perspective. The three major transitions listed above—prokaryote to eukaryotic cell, eukaryotic cell to multicellular individual and multicellular

individual to individuated colony—share some features, both in terms of the process that produced them and the results. All involve hierarchy, the combining of organisms at a lower level to form a new, higher-level entity. All involve natural selection acting on the higher-level entity to produce an individual at that higher level. All involve significant division of labour among the lower-level organisms. And all involve what I have elsewhere called a ‘complexity drain’, a loss of physical parts within the lower-level organisms [6,7].

I have described this pattern as an ‘evolutionary syndrome’ [8], arguing that there is some reason to think it is shared across all or most of the significant transitions in organismal hierarchy over the history of life. That analysis did not include humans, however. So here I raise the question of whether, from this large-scale evolutionary perspective, humans fit the same pattern.

Some disclaimers are needed. First, the mission of this paper is not to argue that human societies have not achieved a transition in individuality. It takes no strong stand on that. The mission is to express scepticism. The title was chosen carefully. Second, the issue here is not whether the advent of human societies was a major event in the history of life. It undoubtedly was. The issue is individuation at the social level. Third—and this is important—the issue is not solely whether a significant level of individuality has been achieved. Rather, it is whether or to what degree *the process has been the same*, driven by the same forces and following the same trajectory, as the other major transitions in the history of life. It is whether human society fits the pattern of the larger syndrome, whether it belongs on the same list as the established major transitions. It is possible that human societies have made the transition to a new level of individuality but have done so via unique mechanisms, driven by unique sets of forces, with unique consequences [9–12]. And in that case, it is not clear that my four reasons for scepticism apply. Thus on account of this macroevolutionary perspective, the issue here is different from the one that has been addressed in most of the human social evolution literature in the years following the Maynard Smith and Szathmáry book [1], different from and orthogonal to it. Fourth, I do not address the possibility that a human transition in individuality is underway but is still incomplete. The relevant comparison group, for my purposes, is the group of non-human transitions in which selection has produced extensive individuation. And the claim will be the rather modest one that to a biologist steeped in the earlier transitions—to the eukaryotic cell, to multicellularity, and to coloniality in marine invertebrates and social insects—humans do not look like they have arrived, nor indeed like they are even on the same road.

Fifth, mode of inheritance is not relevant here. In social insects and marine invertebrate superorganisms, the mode of inheritance is generally understood to be genetic, in contrast with human societies which take advantage of non-genetic mechanisms, i.e. learning and cultural inheritance. Of course, humans have genetic inheritance as well, and epigenetic factors were certainly at work in the evolution of animal societies, in particular environmentally induced heterochrony producing rapid differentiation among lower-level individuals in a single generation [13]. (The genes versus environment distinction or the genes versus culture distinction is never a clean one.) In any case, what matters here is that the driving force, selection, whether genetic or cultural, can produce individuation under either mode of inheritance ([10] and references therein;

[14]). And as will be clear shortly, all four reasons for scepticism apply with the same force under both. Again, genes versus learning and culture is not at issue here.

Finally, the discussion of colony-level individuation, across all taxa and over the history of life, long predates the Maynard Smith and Szathmáry book and any notion of ‘major transitions’ (e.g. [15]). The modern version of this discussion began in the 1960s and 1970s in studies of social insects [16,17]. Less well known is that at about the same time, there was in palaeontology an explosion of interest in coloniality in marine invertebrates, some of which rival the social insects in degree of sociality (e.g. [18–30]). In the 1990s and 2000s, the problem of coloniality was taken up again, both in biology (e.g. [31–34]) and palaeontology (e.g. [35–39]). But the most recent studies have mostly focused on one of three groups of transitions, the cell–multicell, social insect and human transitions. Some work has been synthetic, crossing the lines among these groups and encompassing wide swaths of evolutionary history (e.g. [11,12]). But the work on marine coloniality has been mostly sidelined (although see [13,40,41]) and will be unfamiliar to many modern students of the subject. Thus, one of the missions here is to nudge readers toward that literature. In any case, for those studying the three groups of transitions currently considered more charismatic, this paper offers a view from outside, a view from another corner.

2. Individuation

According to Maynard Smith & Szathmáry [1,3], the major transitions have two defining criteria. They are transitions in which a new higher-level individual emerged or there was a change in the way information was transmitted from one generation to the next. The concern here is only with individuality [42,43].

But what is individuality? In an excellent series of papers, Ellen Clarke [44,45] lists a number of features that have been taken in the literature to be defining of individuality: reproduction, life cycles, genetics, sex, developmental bottlenecks, germ-soma separation, policing mechanisms, spatial boundaries or contiguity, immune response, fitness maximization, cooperation and/or conflict, co-dispersal, adaptations, metabolic autonomy, and functional integration. I do not adopt any one of these here, but will simply note that all represent some functional capacity and all are therefore likely the product of natural selection. And thus my own understanding of individuality is consistent with this approach: higher-level wholes, consisting of multiple lower-level entities, are individuals to the extent they have been acted upon directly by natural selection [45]. Absent selection at the level of the whole, the higher-level whole remains a mere aggregation, an entity with a minimum of individuality [45]. And the greater the duration or intensity with which selection has acted, the greater the degree of individuality. So in this view, the features above do not define individuality, but insofar as they are the product of natural selection, they are indicators of it. There are other indicators, of course (e.g. [12]). In an earlier attempt to find indicators of individuation that would be visible in fossils, I identified three: aggregation among lower-level entities, division of labour (beyond sexual division of labour), and the presence of what I called intermediate-level parts, structures like tissues and organs that have been interpolated between hierarchical levels [37,46]. And later in this paper, I will add

another, what I have called the complexity drain. These indicators, taken together, can be understood as proxies for selection, enabling us to evaluate degree of individuation in specific, concrete cases. For example, it enables us to say that the individuality of a multicellular animal like a starfish, sporting many of the above selection-generated features, is quite high, while the individuality of a multicellular alga like *Volvox*, with few of them, is quite low.

This approach is not ideal. Ideally, we would have formal criteria for the operation of selection at each level [32,47–50], along with a quantitative assessment of intensity of selection at a given level [51]. But in the absence of appropriate data, proxies like this may be the best we can do.

Again, the issue here is the degree to which humans have followed the standard route to social individuality, the route followed historically in other taxa. For this purpose, there is no need here to precisely define the society level. It could be the tribe, the clan, the village, the nation state or any of a number of others. The ambiguity is permitted, I think (and hope), because the reasons for scepticism apply to all of them, albeit not necessarily equally.

3. The four reasons

What follows is a summary of the four reasons. Further explanation is added in the later sections. The first two are reasons in theory, raising the question of whether the processes considered necessary for higher-level individuation have been present and powerful in humans.

- (1) Individuation is the degree to which selection has acted on an entity at a given level, and it therefore presumes the existence of an entity on which selection could act. But the cross-cutting interactions that are pervasive in human societies tend to undermine the entitiness of social units and therefore to undermine individuality. A related point has been made by Stearns, who suggests that in humans the major transition to a social individual may have stalled when ‘group boundaries became fuzzy’ [52, p. 2277].
- (2) Human societies undoubtedly constitute a level of selection, to some extent, but natural selection operates in three modes—the persistence, growth and reproductive success modes—and only the third mode is expected to produce the complex adaptations that characterize a fully individuated higher level. Human societies seem to evolve mainly in the persistence and growth modes.

The next two reasons have to do with results. They raise the question of whether the major phenotypic changes that have characterized the transitions in individuality in non-human organisms over the history of life also occurred in humans.

- (3) Highly individuated entities are marked by a commitment to division of labour, in which lower-level individuals become morphologically differentiated and irreversibly specialized for particular tasks, but in human societies that differentiation is behavioural and often reversible.
- (4) There is strong evidence that selection on a higher-level individual tends to drain complexity, to drain parts, from the lower-level individuals that constitute it. For example, in the transformation of some ancient bacterium into a mitochondrion, selection acting at the level of the

eukaryotic host removed many of the genes from mitochondria. Also, cells in highly individuated multicellular organisms have fewer internal parts than free-living protists [6]. The principle applies generally, across all levels, but it is not clear that such a drain occurred in humans.

(a) Reason 1: overconnectedness

A society cannot be an individual if it is not first an entity, a separate existence, a ‘thing’ of some kind on which selection could act. In other words, the question is whether a society exists at all, whether it is an entity that even has the potential to be an individual.

So what is an entity? Consider this approach. An entity is a set of elements that are well connected to each other, but less well connected to elements outside the set [6,53]. Thus, the drawer of a dresser is an entity in that the molecules in the wood of the drawer are well connected to each other and less well connected to molecules in the frame of the dresser; in other words, they are somewhat isolated from the rest of the dresser. By this understanding a piece of chalk is an entity in that the molecules of carbonate in the chalk are relatively well bonded to each other and poorly bonded to the molecules in the air around it, or to the molecules in the hand of a person holding it. An online chat group is an entity, to some degree. This last example is telling. Connections can take the form of bonds, but they can also be interactions of some other kind. And entities need not be solid objects with hard boundaries. Further, entities can be temporary. A chat group is an entity for however long the interactions among the individuals are ongoing, and it ends when they stop. Finally, this approach raises the possibility of quantification. Entity-ness comes in degrees, and graph-theoretic measures could be developed that are a function of the pattern of interaction and isolation.

The point here will be that the major transition is a story of individuals joining to form higher-level entities, in other words hierarchy, and overconnectedness destroys hierarchy. A box of chocolates is a hierarchical structure consisting of individual parts, chocolates, nested within a larger whole, but that hierarchical structure weakens if the chocolates start to melt and run together. A fungus in which the walls between the cells have broken down, producing a single cavity with a free flow of cytoplasm (a syncytium), is no longer multicellular. A clique at a party is to some degree an entity within a whole, where the whole is the larger party, but as the members of the clique start to chat with people outside the clique, that hierarchical structure breaks down.

Notice that the question of entity-ness is logically prior to the question of individuality. Entities can arise through purely physical processes. Then, once they have arisen, selection can transform them into individuals. But if a society is not first an entity then selection cannot transform it. Interestingly, and consistent with this, it is known that in marine invertebrate colonies, division of labour tends not to arise when lower-level individuals are highly connected with each other [54]. This makes sense in that selection drives division of labour, and without some degree of isolation among lower-level entities, there is nothing for selection to act on.

Now it could be that certain human associations are good entities. Candidates for entities include kin groups, tribes or villages, professional associations, trade unions and guilds. A homeowner’s association, a parent–teacher organization, or a

neighbourhood listserve might be an entity. At a much larger scale, a culture or a nation state might be an entity. For all of these, it might seem that internal integration is considerable—that interactions among the people within the group are many and strong—and that there is a fair amount of isolation—that interactions outside the group are fewer or weaker than interactions inside the group. But in the absence of appropriate connectivity data, it is easy to be sceptical. From my own experience, most human associations seem only weakly entified. I check my neighbourhood association listserve about once a week. My main professional association meets annually. My commitment to these groups in terms of number and intensity of interactions is weak. And it is doubtful that they would be identifiable as entities in a graph showing all interactions. Families might seem to be more clearly entities, but then we run into the problem of non-coincident boundaries. Families span village boundaries. Likewise for many professional groups and religious sects. Trade associations cut across nation-state and cultural boundaries. In the first world, at least, most individuals participate simultaneously in multiple and partly overlapping social units. I might be simultaneously a member of my family, my tennis club, my department, the county school board, Costco and so on. Cross-cutting interactions are frequent and dominate the pattern of connectedness. At least in the modern world, most of us participate in an enormous number of cross-cutting interactions [55]. And on account of these, most human associations are poorly integrated and/or isolated, and therefore only weakly entified, which undermines hierarchical structure.

Compare this situation with the relatively neat nesting of parts within wholes in biology—organelles within cells, and cells within tissues and organs. In these, the entities are physically distinguishable, relatively constant, and mostly well bounded, often with membranes. Compared to the hierarchical structuring evident among entities in the evolutionary individuals that arose in the major transitions, human hierarchical structure seems quite vague.

A caveat: obviously human societies involve hierarchy in some sense. For example, we have command hierarchies, like armies. But these are not nested. Captains command sergeants but sergeants are not physically nested within captains. Only physically nested hierarchical structure is relevant here.

All of this has been impressionistic. But data on numbers and patterns of interaction could be collected, and graph-theoretic measures of entity-ness applied to assess degrees of hierarchical structure. And then we would need to compare various candidates for entities in humans with free-living protists and with cells within a multicellular organism. Gathering such data is not a trivial undertaking. Doing so would involve fraught decisions about what constitutes a connection and how to count connections. But it could be done. And doing this would help to calibrate our somewhat fallible intuitions about entities. A nation state might turn out to be less of an entity than one would imagine. A family might turn out to be more. Or the reverse. We should be prepared for some surprising findings.

(b) Reason 2: selection in growth and stability mode is weak

Selection operates in three modes: persistence, growth and reproductive [13,40,41,56–58]. In reproductive mode, individuals with a greater propensity to survive and reproduce

leave more surviving offspring, and their descendants replace those with a lower propensity. This is the conventional understanding of selection.

Selection in growth mode is different. A clonal aspen variant spreading on a hillside, or a grass variant spreading in a field, is fitter than—and will replace—other variants if it simply grows faster than they do. Likewise a coral variant is fitter than its competitors if it is able to channel more of its surplus metabolic energy, beyond what is needed for maintenance, into growth. Likewise, albeit less intuitively, a single individual, such as a whale, that is able to channel more energy into growth is fitter than its competitors. In pure growth mode, fitness is fatness. For selection in this mode (and indeed generally), fitness is success in the competition for resources, more specifically for energy [56], and the entity with a propensity to commandeer more of it succeeds, on average. For selection in growth mode, there is a critical assumption, namely that neither competitor is reproducing, or if they are, they have an equal propensity to leave surviving offspring.

Finally consider persistence mode [58]. A protist might be fitter than its competitors if it is able to encyst for long periods of time and thereby survive longer. Its competitors go extinct, perhaps by chance, as all species inevitably do, while the fitter individual persists.

Selection operates in all three modes, simultaneously, in all organisms, but the three modes are not equal in their effects. The reproductive mode is widely acknowledged to be the source for complex adaptations of every sort, at all levels of the organismal hierarchy, over the 3.5 billion year history of life. From metabolic pathways in bacteria to cytoskeletal mechanics in protists to hormonal and circulatory systems in multicellulars to social organization in colonial invertebrates, all are assumed to be the result of selection in the standard reproductive mode. What makes the reproductive mode so powerful in the generation of complex adaptation is the massively parallel process of generating and selecting for successful variants. Each reproductively produced individual is a potentially successful variant. And if the reproductive process is sexual, new successful variants can spread quickly in a population, with large numbers of new combinations of variants tried out in every generation. By contrast, selection in growth mode is serial. Successful variants are those that lead to greater growth, and these can arise, for example by somatic mutation in a single stem of an aspen clone, but they spread slowly, limited by the growth of that single individual. Finally, for selection in pure persistence mode, if there is no growth or reproduction, the accumulation of adaptive variants is also a serial process, but again limited to a single, highly stable, enduring individual. That individual can certainly change, vary, in ways that are by chance adaptive—that is, in ways that produce greater persistence—but the trajectory toward the production of complex adaptations will be very slow indeed.

So in what selective mode do human societies evolve? It is hard to see human societies as reproducers. They do reproduce sometimes, for example by fissioning. And they spall off what might be thought of as propagules, a dominant theme of the colonization of the world by western nation states in the past few hundred years, for example. But for the reproductive mode to generate complex adaptations, ideally reproduction would generate larger numbers of offspring. Each human society would have to produce many daughter societies. And

it seems hard to argue that that happens very often in human evolution. Most human societies probably produce none. Rather societies seem to operate predominantly in growth mode, by spreading. In any case, whether we think of them as generating offspring or growing, it is clear that the rate of reproduction or growth is very slow, and that human societies are not able to take advantage of the massively parallel accumulation of variation that is so essential to the production of complex adaptation. So if, as argued earlier, strong selection is necessary to produce individuation, to transform a mere aggregate of lower-level individuals into a higher-level individual with complex adaptations like division of labour, it seems unlikely that human societies can be highly individuated. The process needed to drive this transformation would simply have been too slow, the intensity of selection favouring it too weak.

Again, these judgements are impressionistic. For objective assessments, we would need not only data on rates of reproduction, growth and survivorship of human societies, but the equivalent data for organisms that are thought to have undergone major transitions.

(c) Reason 3: weak division of labour

Selection might favour division of labour for a number of reasons. A higher-level individual with two specialized component entities, one performing task A and the other doing task B, is able to do A and B at the same time. Another advantage is specialization. Division of labour allows the entities within a larger whole to become better at what they do. And there is also body size. Becoming large is often advantageous, but it brings new constraints, some of them solvable by dividing labour [59].

In the recognized major transitions, the amount of division of labour is considered an indicator of the degree of individuation. A mammal with hundreds of cell types is considered more individuated at the multicellular level than a sponge with only six cell types [37]. An ant species with four caste types (e.g. *Atta*) is considered more individuated than one with no differentiated castes (e.g. *Amblyopone*). Presumably the same would be true of human societies.

Two arguments are relevant here:

(i) The first arises from a model developed by Simpson [40] showing that reproductive division of labour is critical in major transitions. Without reproductive division of labour, each new higher-level individual must arise from a subset of the entities that comprise the higher-level whole, in other words, a sample of the parent. And if the propagule produced by this sampling is large, it is likely to contain some defective entities present by chance within the parent. A common solution is for the higher-level individual, the parent, to maintain a small set of dedicated reproductives, each competent to generate a new higher-level individual. If the number of reproductives is small, then the chances are good that none will be defective, and therefore the offspring arising from them will not contain any defectives, regardless of their frequency in the larger parent. One version of this strategy, discovered often in evolution, is called sequestration of the germ line [60]. Once reproductive division of labour is established, further specialization becomes possible among non-reproductives. For a multicellular organism that means many cell types, and for a colony or society,

it means multiple castes, with cell types or castes arising *de novo*, each generation, from a dedicated reproductive.

Examples are easy to find in colonial organisms. Coral colonies do not have specialized reproductives and have essentially no division of labour. Bryozoan colonies do have specialized reproductives, and they also have multiple specialized zooid types, some for defence and others for feeding. Simpson found that the pattern is quite robust, strongly present across a sample of thousands of social or colonial taxa.

For human societies, then, the issue is the degree to which humans have reproductive division of labour, the stage setter for further, complex division of labour. And again I do not have the answer. But impressionistically, reproductive division of labour in human societies seems weak. Reproductive effort is concentrated in females, as in most sexual species, and further concentrated in a 30-year period of women's lives. But women remain omniscient throughout their lives, sometimes able to perform most non-reproductive tasks—both for themselves and for the society as a whole—even while children are gestating and being raised. Further, reproductive effort is not limited to women. Indeed, in many and perhaps most societies, male investment in offspring is considerable. Thus, the situation in human societies is a far cry from the dedicated germ line we see at the cellular level in, say, mammals, where sex cells have very limited non-reproductive functionality, and from the dedicated reproductive functionality we see in some social-insect queens. Indeed, in humans, any small group—randomly sampled from the population—will probably include some females and can therefore constitute a viable propagule for the larger society.

(ii) The second argument has to do with the degree of commitment to specialization in general, not just in reproduction, exhibited by the entities within a larger whole. In the most highly individuated animal colonies, entities commit early in life to a specialized role and remain in that role for life, often acquiring a permanently differentiated morphology that suits that role (Anderson & McShea [61] and references therein). In less individuated colonies, the commitment is non-existent—i.e. no specialization at all—or temporary, with entities changing in a systematic way from one specialized role to another as they mature, what is called temporal polyethism.

What is the degree of commitment to specialization in humans? I have not seen data that would support any firm conclusions, but my impression is that, compared to highly individuated social species, our commitment is unimpressive [62]. Many social-insect species have permanent morphological castes, as do marine invertebrates like bryozoans and certain hydrozoans. Now there is clearly some level of specialization in humans. Certain job descriptions preferentially draw certain phenotypes. In modern western societies, jockeys tend to be small, basketball players to be tall, and bar bouncers to be large and muscular. If we include jobs requiring specific psychological capacities, and those requiring specialized training, examples could be multiplied endlessly. What's more, commitment to a given line of work is often long term, and radical changes in profession become more difficult with age.

On the other hand, administrators seem to be able to move effortlessly among a wide range of job descriptions. And of course, even where specialization is extreme, radical change remains a possibility for some. The occasional fireman becomes a piano player. Finally, even if permanent specialization were

the norm in contemporary first-world societies, it may not be in, say, hunter–gatherer societies, where individuals often seem more nearly omniscient. In offering these evaluations, I am out on limb, but my larger point is surely right: the degree to which human social roles involve permanent specialization is highly variable, both among individuals and tasks and among societies. Thus, compared to most ants, bryozoans and other species forming highly individuated colonies, our commitment to specialization is unimpressive. Likewise in comparison to cells in large highly individuated multicellular organisms. Stem cells in a baboon may remain omniscient, but the vast majority of cell types do not interconvert. A liver cell never turns into a nerve cell. By this standard, our commitment to specialization is negligible.

Again, the perspective on humans offered here starts with the major transitions in non-human organisms. And the claim is not that humans do not divide labour. Indeed, it is possible that our flexible division of labour is superior to the permanent version found in major transition organisms. The point is only that this flexibility does not fit the pattern of other major transitions.

(d) Reason 4: weak or non-existent complexity drain

Cells in multicellular plants and animals have fewer parts, fewer internal macroscale structures, than free-living, single-celled protists ([6], see also [8]). The process that produced this reduction is what I have called a ‘complexity drain’ [6], and it was likely the result of selection favouring the streamlining of function in higher-level individuals. A free-living protist has to do everything for itself: feed, defend, propel, reproduce, etc. And to perform these many functions, it needs many parts. The planktonic unicellular *Pedinella*, for example, has many different types of macroscale structures, including two different types of flagellum, a chromatophore, a nucleus, mitochondria, tentacles, contractile vacuole, food vacuoles, and so on, each with a specialized function. By contrast, a given cell in a complex multicellular organism has to do very little. If it is a skin cell, for example, its main function is simply to attach to other skin cells and shield the organism. It does not have to pursue food, because a circulatory system delivers food to its doorstep. It does not have to propel itself, because all necessary movement is accomplished by the larger organism. And reproduction is handled by a different cell type within the whole, the germ line. And in fact, these cells have fewer parts than most protists. Blood cells typically have even fewer, some with no macroscale parts at all. The complexity drain also operated in the transition to the eukaryotic cell, e.g. the loss of genes in the bacterial ancestors of mitochondria. And there is some evidence that it happened at the colony level. Some social-insect workers lack ovaries. In sum, the argument here is that part loss is an indicator of selection acting at the level of the larger whole, favouring the stripping of no-longer-functional parts from its component individuals.

As far as I know, there is no formal data relevant to a complexity drain in humans. One could argue that social living should make fewer behavioural demands, and that losses of certain behavioural capacities ought to correspond to the loss of certain brain structures. But surely there have been gains as well. It does seem likely that there was a decrease in human brain size over the past few 1000 years, which could indicate a loss of structures and a decrease in

behavioural repertoire [63]. Also, it has been shown in mammals that domestication produces juvenilization [64], which if achieved heterochronically, by the slowing of development, could involve the loss of terminal brain structures of some kind. And Hare & Woods [64] argue that humans are self-domesticated. But none of this is conclusive. I think that in the near-absence of data, we can only say this: human anatomy has suffered no losses as dramatic as those that occurred in the origin of multicellularity. To dramatize this, compare a human individual in a modern society to the sieve tubes in a complex multicellular organism, a vascular plant. Sieve cells have hardly any parts, their needs supplied by adjacent companion cells. Finally, it is worth pointing out if modern humans are missing parts, they are unlikely to be parts critical to survival. We are physiologically (and perhaps psychologically) capable of surviving alone in the wild, outside the social ‘body’, which is not true of any of our cells, so far as we know.

4. Conclusion

There are reasons for scepticism about a human transition in individuality. As discussed, the point of this paper is not to make any strong claim one way or the other, but rather to raise doubts, especially those that arise from consideration of the other major transitions in the history of life. Based on those comparisons, I want to draw attention to two alternative, and mutually exclusive, conclusions: (1) humans have not proceeded very far toward individuality at the social level and are unlikely to proceed very far in the future, given the expected weakness of selection at that level; or (2) if humans have advanced significantly toward individuality at the social level, they have done so by a very different route than the earlier major transitions at the colony level, sufficiently different that the markers that characterize these other major transitions are not present.

Regarding alternative 1 above, it is worth noting that some others are also sceptical, including Stearns [52], who raises the possibility that human societies have not achieved a high level of individuality, and Kessebir [55], who approves of the superorganism metaphor to describe certain features of human societies but offers reasons to think we have not reached that level in all respects. Still, some are more confident that a human major transition is at least underway and will rightly point out that the evidence offered here against one is mainly impressionistic. That is a reasonable complaint, and one that points to the need for more data. Each of the four reasons will need data of a different sort. For reason 1, overconnectedness, the identification of connections will need to be operationalized, and then connections appropriately weighted, producing a connectivity graph, and then a graph-theoretic measure of degree of hierarchical organization will have to be developed and applied. For reason 2, selection in growth versus reproductive mode, the distinction between reproduction and growth will need to be operationalized, and data gathered on the frequency of each in human societies. For reason 3, division of labour, criteria will need to be developed to measure degree of, and permanence of specialization. And for reason 4, a complexity drain, we simply need to count parts. The complexity drain is expected to produce reductions in all part types, behavioural as well as morphological [6], although counting

morphological parts is obviously more straightforward and may serve as a proxy for total part count. In any case, parts will need to be operationalized (e.g. [6,53]) and then counted within individuals, and counts then need to be compared among human societies and among hominid species. None of this is trivial to do. But all of it is doable.

Also regarding alternative 1, I will add that if the notion of a partial major transition is taken seriously, a natural next step for the human case is to assess how far it has proceeded. In a paper some years ago, I developed a scale of what I called ‘minor transitions’ ([65], see also [66]), along with criteria for establishing whether a collective had achieved each minor sub level. For example, the lowly green alga *Gonium*, achieves the first minor level by virtue of forming an aggregate, something its solitary relative *Chlamydomonas* does not do. And *Volvox*, a green alga, achieves the next minor level by virtue of having morphological differentiation among its cells, two cell types. It also reaches the third minor level by having some of its cells arranged spatially, in an analogue of a tissue or organ, what I call an intermediate-level part. These are parts that are larger than a single cell but smaller than the whole organism. For *Volvox*, this is its outer shell of flagellated cells. (See [65] for a discussion and justification of the criteria for each minor level.) This is just one possible approach. Other metrics could be devised.

Regarding alternative 2 above, nothing I have to say here contradicts the various proposals that have been offered for how a human major transition might have proceeded differently, compared to other moves to coloniality. For example, it does not contradict the intriguing suggestion by Andersson & Törnberg [11] that some process analogous to the formation of the first cell was involved, producing a series of

intermediate steps with structural similarities to early human societies, and involving no direct selection initially on the social whole.

Also in connection with alternative 2, a point needs to be made about the way we refer to these transitions. If human societies have become individuated, whether strongly or to some significant degree, but did so by a route that is very different from other sociality transitions, driven by unique forces and with unique phenotypic consequences, one can reasonably wonder whether the same language is appropriate for both. If bryozoan sociality has hardly anything in common with human sociality, other than the degree of individuation achieved, do we want to call them both by the same name, major transitions, implying a deep commonality that may not exist? I am not saying we don’t, just—as in all of the above—raising the question.

Finally, I would point out that the reasons for scepticism offered here are quite general and apply to any of the putative transitions in individuality, including the seemingly uncontroversial ones, such as the transition to the eukaryotic cell and some of the transitions to multicellularity. It is beyond the scope of this paper, but it might be worthwhile to re-examine the other major transitions, including the uncontroversial ones, in light of the arguments offered here.

Data accessibility. This article has no additional data.

Authors’ contributions. D.M.: conceptualization, formal analysis, funding acquisition, investigation, methodology and project administration.

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