**Asexual Organisms, Identity and Vertical Gene Transfer**

**Gunnar Babcock, Jan. 31st 2020**

This is the author’s final draft of a paper forthcoming at *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*

§1 Introduction

1.1 Overview

1.2 The fission problem

§2 Identity and phylogenetics

2.1 Identity in biology

2.2 The identity argument

2.3 Why it matters that the models conflict

§3 Objections and replies

3.1 Lateral gene transfer and the tree of life

3.2 Symmetry and functional immortality

3.3 The pitfall of pheneticism

3.4 Track genes, not organisms?

§4 Models and biology

4.1 Which model is the right model?

4.2 Conclusions

References

**§1 Introduction**

**1.1 Overview**

This paper poses a problem for traditional phylogenetics: The identity of organisms that reproduce through fission can be understood in several different ways. This prompts questions about how to differentiate parent organisms from their offspring, making vertical gene transfer unclear. Differentiating between parents and offspring stems from what I’ll call the identity problem. How the problem is resolved has implications for phylogenetic groupings. If the identity of a particular asexual organism persists through fission, the vertical lineage on a phylogenetic tree will split differently than if the identity of an organism does not survive the fission process.

Section 1.2 presents the metaphysical problem of fission and connects this problem to fission in asexual organisms. The second section reviews some of the philosophical treatments of fission in biology (2.1) and offers the main argument of the paper (2.2 & 2.3). Three models are offered which generate different phylogenetic trees by differently construing the identities of asexual organisms. The third section offers responses to some possible objections to the argument by considering certain issues in biology more closely (3.1, 3.2, 3.3 & 3.4). The final section presents some of the strengths and weaknesses of each of the models (4.1), and a summary of the main conclusions of the paper (4.2).

**1.2 The Fission Problem**

Imagine there is a machine that can make a precise duplicate of you. You walk in the machine, black out for a moment and then are is another person in the machine that is identical to you in every possible way. This is a variant of the fission thought experiments that are common in debates about personal identity. The question such thought experiments present is fairly obvious: which of the two people who come out of the machine is you? But there is a further question such fission problems raise. What relations would you have to the children of you and your doppelgänger? Are your doppelgänger’s children also your children, or are they your grandchildren, or perhaps you have some other relation to them? Did you even survive whatever process took place in the machine? Puzzles about fission raise questions about identity, but they also present problems for determining ancestry and lineages.

Fission thought experiments, like the one above, are generally couched in terms of science fiction. Yet, such fission problems are far from hypothetical. In fact, the majority of life on the planet reproduces asexually through fission-like processes. So, does a particular asexually reproducing organism, like a bacterium, survive the fission process? Biologists don’t seem to give this question much attention. Instead, they often consider one of the post-fission organisms to be the “mother” and also treat both as “daughters”. For example: “a pairwise comparison shows that the difference in the growth rate between the old pole sibling (the mother cell) and the new pole sibling (daughter cell) increases with the increasing age of the mother” (Stewart, et al., 2005, p. 297). In the quotation above the mother cell and one of the daughter cells are treated as sibling cells – but a single organism can’t be its own daughter, at least not without drastically altering the normal relations the two terms denote and undermining the very notion of generations.

We might also wonder how to trace the lineages and lines of descent of this bacterium. This paper is primarily concerned with that question, as it has implications for the phylogenetics of asexual organisms. In essence, Godfrey-Smith’s observation that “a number of people have noted that, from a formal point of view, asexual reproduction of one offspring plus the death of the parent (or fission plus death of a daughter) seems not much different from continuation of the parent” (Godfrey-Smith 2009, p. 104) is mistaken when it comes to phylogenetics. There is a formal difference. If a bacterium survives fission and has fifty daughters, all of these daughters are members of a single generation.[[1]](#footnote-1) But, if a bacterium cannot survive fission, and we count down fifty fission events, the bacterium that comes into existence in the last fission will be forty-nine generations removed from the original bacterium. Amplifying this difference over millions of bacteria greatly alters how the branches on the tree of life might be traced.

**§2 Identity and phylogenetics**

**2.1 Identity in biology**

Fission has not been a widely discussed topic in the philosophy of biology.[[2]](#footnote-2) While philosophers have occasionally considered fission in microorganisms (particularly amoebas), fission problems are usually used in the service of arguments related to personal identity (cf. Rorty 1976).[[3]](#footnote-3) When fission is considered in the philosophy of biology, the discussions are not particularly extensive. Hull (1978, p. 345) and Sober (2000, p.155-6) say that an organism “ceases to be” after certain forms of fission, e.g. transverse fission. While Hull doesn’t provide an argument for why this is should be the case, Sober argues that an organism necessarily ceases to be post-fission because of the principle of identity of indiscernibles (i.e. “if, for every property *F*, object *x* has *F* if and only if object *y* has *F*, then *x* is identical to *y”* [Forrest, 2016])[[4]](#footnote-4) Yet, both Hull and Sober use fission as a segue into the species debate. Olson (1997) gives more consideration as to whether an amoeba dies when it divides during fission. He argues that an amoeba necessarily dies when it divides because the process undermines the organism’s physical integrity, but his argument is in the service of a broader discussion on biological death. More recently Bourrat (2015) considers asexual reproduction wherein he discusses two possible ways to model Earnshaw-Whyte’s evolution by natural selection which depend on “what is understood by ‘parental’ and ‘offspring’ entities” (Bourrat 2015, p. 891). Yet, Bourrat’s consideration of how these models can vary depending on how we understand parent/offspring relations, pertains to heritability. Thus, all of these accounts of biological fission are adjacent to the metaphysical fission question raised in section 1.

Some of the other considerations of fission in biology focus on the process itself. Godfrey-Smith (2009) argues that binary fission is a form of reproduction while others argue that it is more akin to plurifaction (e.g. Gould 2002, p. 611), though they agree that the process results in the emergence of new individual organisms or entities. Godfrey-Smith treats binary fission as a reproductive process because the entities involved in the process create new entities that possess a “physical separateness” from those that generated them (Godfrey-Smith 2009, p. 85). These discussions tend to lead to questions about biological individuality.[[5]](#footnote-5) This is due, in part, to claims that such processes are not reproductive processes at all but rather processes of development through which entities, like genets, merely grow (e.g. Janzen 1977). According to such views there are no new organisms (or other sorts of biological individuals) that come into being so long as genetic fidelity is maintained. Others argue that certain microbial communities are perhaps better considered as individuals or organisms themselves (cf. Wilson and Sober [1989]; Queller and Strassmann [2009]). It is obvious that the ways in which we understand processes like binary fission can blur the line between reproduction and development, which then informs positions on biological individuality (Griesemer 2014). Yet, to the best of my knowledge, no one has directly considered how questions about biological individuality and reproduction affect phylogenetics and ancestral relations.

When it comes to microbes, biologists seem not to give much attention to how identity[[6]](#footnote-6) affects parent/offspring relations either. This could be rooted in mistaken assumptions made in early microbiology about the relations between microbes, not unlike the mistakes made by early microbiologists regarding microbial sexuality.[[7]](#footnote-7) This has led some studies use a parent/offspring model in fission events, others use an offspring/offspring model in fission events, while others waffle between the two. In essence, their approach seems similar to Godfrey-Smith’s thought that there’s not much of a formal difference between the birth of an offspring verses the continuation of a parent.

Intuitions tend to guide the distinction between parents and offspring in how reproductive/developmental processes are understood. In the case of organisms that reproduce through binary fission the inclination has often been to treat post-fission organisms as siblings, where the parent continues to exist as a daughter. Yet, in the case of multicellular life, like ramets or genets, intuitions tend to go in the opposite direction - we think that the mature tree from which the cutting came is the parent while the plant that grows from the cutting is its offspring.[[8]](#footnote-8) In the case of fusion, e.g. grafting one plant to another, we don’t even consider the process reproductive, but rather a process of development where there is just one organism. I do not want to advocate that one of these positions has got the metaphysics right. My point is that questions about whether a biological process is developmental or reproductive extend beyond biological individuality. The debate over biological individuality has implications for phylogenetic systematics. This is because if the aim of phylogenetics is to demarcate evolutionary groups via the descent of common ancestors, then we are obliged to determine what type of process fission is. Which side we come down on changes the number of distinct entities that have existed. This, in turn, changes their relations and the groups that they form. So, even though phylogenetics and genealogy are not engaged in the same enterprise, when the relations between organisms change drastically then the points where speciation occurs or lineages are formed and clades are drawn will change as well.

The following example is a clear illustration of the point above: Is binary fission a reproductive process that leads to new organisms or it is a developmental process that doesn’t generate any new individuals? Consider what follows if binary fission is a developmental process wherein a single, monolithic, spatially discontinuous genet grows. If this is the model used to track relations, then the lineages of multiple organisms and discrete evolutionary groups are not being traced. Rather, we’re just tracing the parts of a single individual over time and this tells us nothing about the species’ evolutionary trajectory.[[9]](#footnote-9) As we can see, problems of identity impact phylogenetic groupings.

Sections 2.2 and 2.3 will present the main argument of this paper. The conclusion of this argument is that how we understand the identity of asexual organisms, like certain microorganisms, can lead to different phylogenetic groupings. The vertical transmission of genes and ancestry work out differently depending on how we understand identity.

**2.2 The identity argument**

This section contains the primary argument of this paper, which I’ll call the “identity argument”. I will begin by noting that the identity argument, as presented in this section, is idealized in two ways. First, it sets aside important issues that have been widely discussed in how to understand the tree of life, like lateral gene transfer (LGT). I have done this to explicate the argument with greater clarity; LGT and the tree of life will be addressed in section 3.1. Second, this section and the next set aside other biological objections that could be raised against the idea that identity has implications for phylogenetics. These objections are: i) that offspring organisms can be distinguished from their parents, i.e. that they are not actually symmetrical, ii) that speciation cannot occur when there has been no change in an organism, and ii) that phylogenetics traces genes, not organisms. These objections will be addressed in sections 3.2, 3.3 and 3.4.

Recall the fission problem outlined in section 1. Following that problem, let’s say there’s an individual bacterium with a particular genetic makeup - call it “*A*”. *A* reproduces through fission by splitting and we’re left with two fairly similar or “symmetrical” bacteria. This leaves us wondering whether *A*’s fission results in *A* and *B* or in *B* and *C* (i.e. does *A* maintain its identity through fission)? Given this is the problem that fission presents in individuating certain asexual organisms, there are three ways we might model the ancestral relations between organisms. One option is that *A* maintained its identity while generating one offspring. A second option is that *A* lost its identity in a process that might be something like a death, while creating two offspring. Finally, it might be that *A* remained part of a single entity comprised of multiple bacteria.[[10]](#footnote-10) Using each of these views of identity, how we depict the descendants of the bacterium *A* ends up differently. Thus,depending on which of these views of identity is adopted, we get different trees of descent. Below are diagrams representing each of the three models, respective to how they treat identity.

Figures 1a, 1b, 1c and 1d: Each letter represents an organism/entity at given stage, where the same letter represents a continuation of the same organism/entity. The lines mark the boundaries of the generations. All organism/entities within a certain boundary are all parts of that generation. The numbers within each boundary indicate which generation the organisms/entities in that boundary belong. For example, in figure 1a, *I, E* and *C* belong to the second generation. Arrows that point away from a letter represent the splitting of an organism/entity that occurs during fission. The letters at the end of an arrow indicate the organism/entity that exists after the split, which is a first-generation descendant of the organism/entity *or* a continuation of the original organism/entity.



 



The first way of understanding identity is the *persisting model* (figures 1a & 1d). In figure 1a, *A* is a single entity that persists in a series of stages to the left, where each stage of *A* is symbolized with ‘A’. In this way, *A* has the offspring *C*, *E* and *I*. And, *C, E* and *I* persist with the type of stages as seen with *A*. However, because the persisting model is actually a polytomy, using the tree structure of figure 1a ends up distorting the model by using the same letter to represent multiple stages of one entity. Because *A* continues on to propagate a possibly infinite set[[11]](#footnote-11) of offspring, an alternate representation of the persisting model (figure 1d) presents the polytomy explicitly. This is the model that should be used if there is a “mother” organism (that is not also a daughter).

We might adopt a second position: the *death model*. On the death model, when *A* reproduces through fission the original parent dies leaving behind two daughter (or sibling) organisms. On this model an organism retains its identity until it undergoes fission. In the diagram (figure 1b), each organism has a single stage before fission and death, thus each letter is symbolized only once on the diagram. In this diagram, *A* has the offspring *B* and *C*. Similarly, *B* has the offspring *D* and *E*. With each new generation, the old generation dies (or ceases to be). This is the model that arguments from Sober (2000) and Olson (1997) support.

The third and last model that can be adopted is odd. It is not a model that is used by biologists who treat microorganisms *as* organisms, but it nonetheless represents a possibility.[[12]](#footnote-12) In this model, when a cell reproduces it creates new entities that have the same identity as the parent cell. Metaphysically, the model depicts the spatial growth *and* temporal stages of a developing entity in a way that has parallels in Bouchard’s (2008) account of the differences between genets and ramets. For example, each symbol ‘A’ at a given generation are parts of *A* at a particular temporal stage. I call it the *multiplying model* (figure 1c). This looks to be metaphysically strange because it means there is a single identity inhabiting what appear to be multiple entities that exist simultaneously.

Each of these models is incompatible with the others for the obvious reason that depending on which position is selected on each of the respective diagrams, a different entity will be picked out.

**2.3** **Why it matters that the models conflict**

The objective of this paper is not to advocate for one model over another or to present a new position in the debate on identity or individuality. Rather, it is to show that the models lead to conflicting phylogenetic trees of descent - the taxonomy of microorganisms and asexually reproducing organisms is problematic independent of other problems that face accurately constructing the tree of life for asexual life. Depending on which model is used, we could end up demarcating the genetic and cellular lineages (and even species memberships of microorganisms) in conflicting ways. To see why, consider what follows if we try to make a bifurcating phylogenetic tree starting with organism *A*.

The persisting model starts with organism *A,* which then divides leading to organism *C* (because *A* remains *A* in the next stage). The death model starts with organism *A*, where *A* will split into *B* and *C,* as *A* has only one stage. On the persisting model there have been a total of two organisms (*A* and *C*). On the death model, there have been a total of three organisms (*A, B and C*). The discrepancy is in part because the persisting model is not, in fact, a *bi*furcating phylogenetic tree (refer to the persisting model as represented in fig. 1d). The models conflict, most fundamentally, on the sheer number of organisms (or entities) that have existed. Continuing to increase the fission events with a bifurcating tree of descent, both models will amplify the discrepancy in the number of organisms; on the second generation the persisting model has a total of four organisms, whereas the death model has a total of seven organisms, etc.

But the difference in the number of total individual organisms is not the real crux of the problem. The problem is, depending on which model is adopted, some of the organisms that occupy the same places on the tree will be put at difference generations of descent, which can alter the phylogenetic relationships between organisms. For example, if we follow a temporal sequence of *A*’s direct daughter offspring on the persisting model (see version 1 [fig. 1a]) we get an indefinite string of organisms beginning with *C, I* and *E* where *C* is, chronologically, the oldest. These are all first-generation descendants of *A*. But if we switch to the death model, *A*’s *only* offspring are *B* and *C*, because on this model the second stage of *A is* *B*. Continuing in this way, *B* reproduces leading to *D* and *D* reproduces leading to *H* and *I*. Thus, on the death model *H* and *I* are four generations away from *A*. On the persisting model, *I* is only one generation from *A*. Different views of the identity will yield conflicting vertical trees of descent.

Despite the conflict that emerges between the different models, we might think it turns out to be trivial. This is because, despite the difference in the number of organisms and the different parsing of generations between the models, it seems as though the clades (or phyla) do not change. Thus, whether one adopts the persisting model or the death model, it would appear as though all of the organisms are still decedents of *A*. But this is a mistake and the conflict is not merely trivial. To see this, we need only move down several fission events on each of the models.

Using the death model, let’s say that something occurs during the fission between *D* and *B* that’s sufficient to consider it a speciation event, whatever that might be (see speciation diagram: death model). Perhaps there’s genetic mutation in organism *D* making *D* genetically different (and distinguishable) from organism *B* because the genetic mutation makes *D*’s morphology and behavior taxonomically distinct from *A*, i.e. *D*’s mutation makes *D* a distinctly new species that is not the same species as *B*. [[13]](#footnote-13) Or, rather than genetic mutation, perhaps the event is an isolation event; some barrier permanently separates organism *D* from organisms *A, B,* etc. This propels organism *D* into a new environment sufficient for allopatric speciation, so *D*’sspecies membership changes. Whatever conditions we might think are sufficient for a speciation event, imagine the event takes place at the fission event that begins with organism *D*. Of course, one might object that without any change in the organism, speciation cannot take place (this objection will be discussed in section 3.3). For present purposes, let’s assume that mere similarity (genetic or otherwise) is *not* sufficient for species membership. Thus, in principle, it is possible for a speciation event to take place between genetically identical organisms. Figures 2a and 2b follow Hennig’s diagram of speciation (Hennig, 1966, p.31).

When the imagined speciation event above occurs on the death model (figure 2b), *H* and *I* are the second generation of the new species. Organisms *A* and *B* are ancestors of *H* and *I* (they are still all part of the same lineage). But notice that organisms *C* and *E* are not a part of *D*’s lineage though they share the common ancestor *A*. Thus, organisms *H* and *I* are members of a different species than organisms *N* and *O*. Similarly, if we carve up the death model into clades, all members of the tree share the common ancestor *A*, but moving down to *D*, only *H* and *I* are members of the clade beginning with *D*.

Now let’s turn to the speciation on persisting model (figure 2a). Note that on the persisting model what would be organism *D* on the death model is instead just a later stage of organism *A.* In fact, organisms *B*, *D* and *H* on the death model are all simply different stages of organism *A* on the persisting model (fig 1d depicts the persisting model without stages).[[14]](#footnote-14) This not only entails that organism *I* is only one generation away from *A*, but there are also numerically fewer organisms on this model. Though there are the same number of symbols on each of the models (nine), there are only five organisms on the persisting model as opposed to the nine organisms on the death model. On this model, all of the organisms represented in the diagram are members of the clade descended from *A*.

Figures 2a and 2b: The symbols in these figures are the same as those in figures 1a, 1b, 1c and 1d, with the addition of the triangular wedge. The triangular wedge represents a speciation event, where organisms that fall on one side of the wedge are members of a difference species than those that fall on the other side of the wedge.





Thus, on the different models, we can see that the fission event that yields organism *I* will give organism *I* different sets of ancestors (and descendants, though they do not appear on the diagrams). The discrepancies between the two models begin from noting the difference in the number of organisms and the generations between them. Remember, as well, that the diagrams represent (at most) only *four* generations. If the theory of functional immortality is true the discrepancies on the models would likely extend over hundreds or thousands of generations. So, on one model we might treat two organisms as being only one generation apart, while on another they could be treated as being thousands of generations apart. This has serious implications for phylogenetics. For example, assume that an organism will, on average, die after having fifty offspring on the persisting model— on the death model, it will have just two.

Figure 3: “2v50” = two organisms or fifty organisms. The numbers following generations are the number of organisms that would belong to that generation according to each of the respective models.



An organism that survives through fifty fission events will have over six million descendants by the fourth generation, while an organism that cannot survive fission will only have sixteen by the fourth generation (see figure 3). The difference between the models means an organism can be placed *millions* of generations apart depending on which model is adopted. As it turns out, the identity of certain asexual organisms matters quite a lot in figuring out their phylogenetic trees of descent, because how ancestors and descendants are determined will affect how evolutionary groupings are determined.

**§3** **Objections and replies**

**3.1 Lateral gene transfer and the tree of life**

An objection to the identity argument might be that it relies on traditional tree-like relations. The more philosophical attention that has been directed towards asexual organisms, the more problems have emerged for the traditional phylogenetic systematics developed for the world of sexually reproducing organisms. Philosophers and biologists seem to agree that the traditional ways of carving up the biological world may not have the right resources to be able to systematize asexual organisms. Some organisms simply defy hierarchical tree-like structures. Thus, it should come as no surprise that there continue to be problems for traditional tree-like models like those used in the identity argument.

A response to this type of worry begins in examining why there are fundamental questions as how to understand the tree of life. These are due, in part, to the mounting evidence that the much of the microbial world share genes laterally (or horizontally). Ford Doolittle (as quoted by Maher [2002]) notes that, “the overall structure of the prokaryotic world could conceivably owe itself entirely to lateral gene transfer.” This is because LGT allows microbes to share genetic material through means other than reproduction. In LGT, genes are shared “laterally” between organisms rather than “vertically” where a parent organism replicates its genetic material, passing it directly to its offspring. The vertical, tree-like structure typically used in phylogenetics can be misleading when applied to parts of microbial genomes that have been transmitted laterally. This is a large part of the reason why phylogenetic, hierarchical trees of life for microbes can be inaccurate and misrepresentative of their lineages (Doolittle 2000, 2009, Doolittle and Bapteste 2007). Because of LGT, “individual molecular trees, whether based on single genes or particular combinations of genes, instead of being mutually supportive and providing cumulative support for a unique branching pattern of evolutionary history, frequently contradicts one another’s story” (O’Malley 2014, p. 82). It appears likely that whatever genetic relations there are between microbes, traditional hierarchical “trees” of life are probably far better convinced of as web-like structures, where organisms may have multiple genetic lineages that converge. For such reasons, the traditional phylogenetic tree of life looks deeply problematic when applied to the majority of life on the planet.[[15]](#footnote-15)

Given the problems that face the traditional trees of life, it may appear as though the identity argument is a non-starter because it is grounded in vertical gene transfer, and so it is flawed because it fails to take into account lateral gene transfer. My response to this type of worry is fairly simple: while lateral gene transfer is prominent between many asexual organisms, there are no asexual organisms that do not share genes vertically as well (i.e. that do not reproduce). And, anywhere there is vertical gene transfer between asexual organisms the identity argument will be a problem if parents cannot be distinguished from their offspring. Thus, the identity argument is a separate and distinct issue apart from the current problems facing the tree of life as it applies to asexual organisms.

**3.2 Symmetry and functional immortality**

Is it really the case the parents can sometimes fail to be distinguishable from their offspring? I believe this type of objection might be the main reason to resist the identity argument. The move is to deny that the fission problem actually exists in biology. After all, most cases of biological fission are asymmetrical cases – which is to say, the post-fission organisms are *not* identical to the other. And, because philosophical fission problems are premised on identical entities, we don’t have worry about identity in biological fission. I believe examining a debate in microbiology regarding functional immortality is helpful in ascertaining how serious this objection may be.

Certain species of microorganisms, such as *Saccharomyces pombe* and *Escherichia coli*, appear to reproduce symmetrically.[[16]](#footnote-16) The clearest example of symmetrical reproduction can be found in the controversial thesis that certain microorganisms are functionally immortal. There is evidence that suggests that the species *E. coli* and *S. pombe* are functionally immortal (Florea 2017). An organism is functionally immortal if it doesn’t age. And, if organisms do not age, parents and offspring appear very similar.

Reproduction in *E. coli* is a paradigmatic case of the fission problem, if there is one, because when a bacterium reproduces through binary fission it leaves behind two “symmetrical” organisms: each organism has an identical genetic makeup and each appears roughly the same. “Symmetry” in microbiology, means that one post-fission organism cannot be established as being an older organism because it shows no differences from the other offspring, e.g. there are no morphological differences, nor does it have a different reproductive rate that might indicate functional aging. A biological asymmetry is when it is possible to identify one as an older “parent” due to differences such as those mentioned above (as is the case with many species of microorganisms). If some microorganisms are functionally immortal and they reproduce symmetrically the consequence is that it is difficult (or impossible) to privilege one of the post-fission *E. coli* bacterium as the original, aging parent organism.

Nevertheless, the biological notion of symmetry is not equivalent to a strong conception of logical identity in philosophy. Thus, on the one hand, this means the fission problem as it is classically raised in philosophy is not equivalent to symmetrical fission in microbiology. Symmetrical biological fission doesn’t entail that there are *no* differences between post-fission organisms. On the other hand, because we’re trying to track ancestors and lineages, it’s not just *any* difference between organisms that is at sake. The more pointed identity question, as it pertains to ancestors and lineages, is which organism is the parent organism (if there’s a parent)? Thus, what property is sufficient for tracking *parental* identity?

How do biologists know that a parent organism survives symmetrical fission and (if it does) what property do they use to determine which one it is? It seems unclear that the methods used by biologists always succeed in identifying a parent organism. The general method used in these studies is to track cell poles proteins. For example, during cytokinesis in eukaryotes, the “old” end of a microorganism moves to one side of the dividing organism so that one of the “offspring” inherits older cell-surface material. But, merely having the ability to track a “pole” between pre and post fission, by itself, doesn’t mean that the pole is sufficient for identifying the parent. Consider that while one side of the cell wall may be chronologically “older”, the thesis of functional immortality states that such organisms don’t functionally age. Thus, locating chronologically older pole cellular surface material doesn’t necessarily create a property sufficient for “parental” identity because it seems quite likely (in fact, fifty-fifty in binary reproduction) that the “old pole” could end up tracking the wrong organism unless we have some reason to think chronologically older cell wall material has some property that is sufficient for parental identity (i.e. a property which signifies functional aging[[17]](#footnote-17)). Therefore, if certain microorganisms are functionally immortal how do we track them? And how could it ever actually be proven they’re functionally immortal? Does the old pole track a parent, or does it go to the offspring? For this reason, symmetrical fission contains a real identity problem.

Up until 2005, the typical position was that most microorganisms are immortal because a single organism appears to persist through fission events and it will continue to do so, so long as its environmental conditions remains favorable. Other evidence suggests there are no truly symmetrical fission events because there is a difference in the rate of reproduction (or fission) between the subsequent offspring.[[18]](#footnote-18) Currently, there are studies that both support and deny the notion of functional immorality (Florea 2017). For example, a study in 2013 supports functional immortality saying, “*S. pombe* does not age under favorable growth conditions” (Coelho, et al. 2013 p.1844). Insofar as there is evidence to suggest that certain microorganisms divide symmetrically, it seems natural to assume that as long as an organism retains its physiological integrity, such an organism has the potential to continue living and reproducing indefinitely… or such organisms don’t survive the fission process. Thus, while it seems the jury is still out on whether the fission problem actually occurs in biology, insofar as there is evidence that some species are functionally immortal, the fission problem is a genuine problem in biology.

I think questions regarding biological symmetry reveal that more work is needed in figuring out what properties are sufficient for parental identity, whether post-fission organisms are symmetrical or asymmetrical.

**3.3 The pitfall of pheneticism**

Another reason to question the identity argument would be if any evolutionarily significant event, like speciation, requires a change between a parent and its offspring. No new species can come about if it’s supposed members have no differences from the species it was supposed to have evolved from. Insofar as change is a necessary condition for speciation to occur (the objection goes) it is always possible to distinguish parents from offspring as this change will be present. Thus, the identity argument fails because while there maybe times parents can’t be distinguished from offspring, those instances aren’t important because speciation could not have occurred. Whenever speciation occurs, it will always be possible to distinguish parents from offspring. I believe this objection fails for the following reasons.

Notable contributors to the species debate (e.g. Hull 1978) have convincingly illustrated that mere similarity, genetic or otherwise, is not sufficient species membership. There is an arsenal of thought experiments about counterpart organisms with distinct lineages that serve to delegitimize purely phenotypical methods of classifying organisms.[[19]](#footnote-19) Phenotypic and physiological taxonomical methods are generally thought to encounter trouble when used as species classification for obvious reasons (cf. LaPorte 1997, Matthen 2009). For a good discussion of these reasons, see Matthen (2009, pp.98-100). In any case, this means that just because an organism doesn’t change post-fission doesn’t mean its species membership couldn’t have changed.

This means that identifying an organism by merely observing its phenotypical traits, morphology or behavior does not serve as a reliable guarantor of its lineage, e.g. cases of convergent evolution have led to many mistaken species classifications and trees of life. And it’s sometimes forgotten that the same is true of genes (Sober 2000, p. 151). A particular sequence of nucleotides that make up a gene might happen to remerge through mutation a millennia apart, but they are not the same gene if they are not casually linked, i.e. descended from the same original strand. Obviously, the odds weigh heavily against such possibilities - if they didn’t, phylogenetics would be a fool’s errand. I don’t mean to suggest that phylogenetics can’t trace real lineages, but this observation has an important point. When it comes to species designation, we’re not sure what heritable changes between generations in genes, morphology, or whatever else tell us. Like the thought experiments mentioned above, we could imagine synthetic biologists randomly creating a sequence of DNA that is identical to some “natural” organism’s genome. But a randomly generated synthetic genome will fail to have a causal connection to its “natural” counterpart genome (Babcock, *forthcoming*). So, in spite of having identical genomes, an organism with the synthetic genome will not necessarily be a member of the same species as the organism with a natural genome.

The upshot of this observation about species is that it’s far from clear what transformations are necessary or sufficient for a speciation event, i.e. where the branches on a tree of life should be drawn. We can make good guesses, but the points that form the actual cleavages that lead to speciation are something of a mystery. Of course, how to determine the points in a lineage to demarcate speciation events are not unique to asexual organisms, but just the familiar species problem. However, in principle, there could be speciation event or a branching on the tree of life during the life of a single, phenotypically or genetically unchanged organism (cf. Matthen 2009). Such an occurrence actually seems quite likely in allopatric speciation. This means there can be phylogenetically or evolutionarily significant events like those described in the identity argument. Until we have an account of what constitutes a speciation event, speciation is a possibility during any reproductive or isolation event.

**3.4 Track genes, not organisms?**

Finally, another way to resist the identity argument is to argue that phylogenetics tracks *gene* lineages rather than the *cell* lineages or organisms. While this seems to be a viable move, I believe the same problem of determining the ancestral relations between organisms reemerges in DNA replication. DNA replicates in a way that presents an uncertainty of which strand should be viewed as the “original” strand, like what is seen in which organism is the parent in biological fission. In DNA replication, it’s not clear which strand of DNA should be considered the original or “parent” strand any more than fissoning microorganisms. This is because during replication the only distinguishing feature between the two strands of DNA that are being “un-zipped” is that one strand is the lagging strand while the other is the leading strand. The leading strand is the strand that is synthesized in the same direction as the growing replication fork. There’s no reason why the DNA that comes from the leading strand should be placed in the privileged position of being a “parent” or the original strand DNA. Both strands will come to have the same formal structure, both will have obtained material bits in the form of nucleotides procured from the surrounding cell and both will have used the external machinery of the cell to complete their structures.

So, I believe the same question of identity applies to DNA replication as much as it does to processes like binary fission. Thus, while the identity argument in this paper has been applied to microorganisms, all of the formal points apply equally to DNA replication. I don’t believe shifting the focus more to the *genetics* than to the *phylo* part of *phylogenetics* helps us escape the identity problem.

**§4 Models and biology**

**4.1 Which model is the right model?**

There are reasons to use one model rather than another given circumstances relating both to metaphysics and to the biology of the organisms in question. For example, when two juvenile cells are the result of binary fission, perhaps we ought to adopt the death model. Unless we suppose that the mature organism which reproduced reverted back to a juvenile stage, there are two new organisms with two new identities. Similarly, when two organisms result from binary fission, but one reproduces at a slower rate than the other, it seems reasonable to adopt the persisting model because slowed reproductive rates is a typical sign of aging.[[20]](#footnote-20) In such cases, it seems reasonable to think a parent organism has been identified. Hull makes remarks along these lines comparing, for example, transverse fission to budding in Hydrozoa (Hull 1978, p.345).

Yet, there are also reasons to think that all of the models are flawed. Consider that adopting the death model would mean that microorganisms die without leaving behind a corpse or decaying when undergoing fission, so the “fission” death of a microorganism looks wholly unlike the death of the same microorganisms under other conditions, e.g. when they lyse in a hostile environment. This could mean that fission might be just as much a process of biological death as it is a process of development or reproduction. If it turns out that when microorganisms die there is necessarily a corpse, it then seems we should use the persisting model. But if some microorganisms are truly symmetrical post-fission, it may be conceptually impossible to specify which post-fission organism is the parent on the persisting model. Finally, the multiplying model also faces trouble because it requires a metaphysical view of identity wherein an individual entity is in multiple places at one time. Thus, while there may be reasons for adopting one model over another because of the type of organisms that are being examined, there are also reasons to think that none of the models has the right metaphysical take on the identity.

**4.2 Conclusions**

I’ve presented various reasons, both biological and logical, to employ one model of identity rather than another. But, ultimately, no model appears decisively better than another for all cases. The biological facts and the organisms being considered matter quite a bit when it comes to determining which model should be used and how the identity of asexual organisms should be construed. The broad point is that more attention needs to be given to identity if we want to construct accurate phylogenetic trees, i.e. vertical gene transfer is another problem in understanding the relations between microbes and asexually reproducing organisms generally.

The more nuanced point is that more attention should be given to which properties are sufficient for biological identity in asexually reproducing organisms. Organisms that reproduce through symmetrical fission will likely require a model quite different than those that can reproduce through propagules. When it comes to asymmetrical, asexual reproduction, thinking that *any* asymmetry between two organisms is sufficient for establishing identity is likely a mistake. Some asymmetries may not track identity.

References:

Babcock, G. (forthcoming) “Are Synthetic Genomes Parts of a Genetic Lineage?”, *British Journal for the Philosophy of Science.* axz046, <https://doi.org/10.1093/bjps/axz046>

Bouchard, F. (2008) “Causal Processes, Fitness, and the Differential Persistence of Lineages”, *Philosophy of Science.* 75: 560-570

Boucher, Y. & Bapteste, E. (2009) "Revisiting the concept of lineage in prokaryotes: a phylogenetic perspective." *Bioessays 31*: 526-536.

Bourrat, P. (2015), “How to Read ‘Heritability’ in the Recipe Approach to Natural Selection”, *British Journal for the Philosophy of Science*. 66: 883-903

Coelho, M., Dereli, A., Haese, A., Kuhn, S., Malinovska, L., DeSantis, M.E., …& Tolic-Norrelykke, I.M. (2013). “Fission yeast does not age under favorable conditions, but does so after stress”. *Current Biology*, *23*(19), 1844-1852

Davidson, D., (1987), “Knowing one’s own mind”, *Proceedings and Addresses of the American Philosophical Association*, 60(3): 441-58

Doolittle, W.F. (1999), “Phylogenetic classification and the universal tree”, *Science* 284: 2124-2129

Doolittle, W.F. (2009), “The practice of classification and the theory of evolution, and what the demise of Charles Darwin’s tree of life hypothesis means for both of them.” *Phil Trans R Soc B 364*:2221–2228

Doolittle, W.F., & Bapteste, E. (2007). “Pattern pluralism and the Tree of Life hypothesis”. *Proceeding of the National Academy of Sciences*, *104*(7), 2043-2049

Florea, M., (2017). “Aging and immortality in unicellular species”, *Mechanisms of ageing and development, 167*, 5-15

Forrest, Peter, (2016). "The Identity of Indiscernibles", *The Stanford Encyclopedia of Philosophy* (Winter 2016 Edition), Edward N. Zalta (ed.), URL = <https://plato.stanford.edu/archives/win2016/entries/identity-indiscernible/>

Ghiselin, M., (1987). “Species concepts, individuality, and objectivity”, *Biology and Philosophy*, *2* (2):127-43

Godfrey-Smith, P., (2009). *Darwinian populations and natural selection.* Oxford University Press

Gould, S. J. (2002). *The Structure of Evolutionary Theory.* Cambridge, MA: Harvard University Press.

Griesemer, J. R., (2014) "Reproduction and the Scaffolded Development of Hybrids," in Caporael et al. (eds), Developing Scaffolds in Evolution, Culture, and Cognition, MIT Press, 23-55

Hennig, W. (1966) *Phylogenetic systematics.* Urbana: University of Illinois Press

Hull, D. (1978) “A Matter of Individuality.” *Philosophy of Science,* 45: 335-60

Janzen, D. H. (1977). “What are Dandelions and Aphids?” *American Naturalist,* 111: 586-9

Kuramae, E.E., Robert, V., Snel, B., & Boekhout, T. (2006). “Conflicting phylogenetic position of Schizosaccharomyces pombe”. *Genomics*, *88*(4), 387-393

Rorty, A.O. (ed.), (1976), *The Identities of Persons.* University of California Press. 17-40

Maher, B., (2002). “Uprooting the Tree of Life”, *The Scientist*, September, 2002

Matthen, M., (2009), “Chickens, eggs, and speciation”, *Nous*. 43 (1):94-115

O’Malley, M. (2014). *Philosophy of microbiology.* Cambridge University Press

O’Malley, M., Martain, W., Dupre, J. (2010), “The tree of life: introduction to an evolutionary debate”, *Biology and Philosophy, 25*:441-453

Partridge, L., Barton, N.H. (1993). “Optimality, mutation and the evolution of ageing”. *Nature* 362, 305–311

Queller, D., Strassmann, J. (2009), “Beyond society: the evolution of organismality” *Phil. Trans. R. Soc. B,* 364, 3143–3155

Queller, D., Strassmann, J. (2016), “Problems of multi-species organisms: endosymbionts to holobionts” *Biology and Philosophy 31* (6):855-873

LaPorte, J., (1997), “Essential Membership”, *Philosophy of Science 64*(1): 96

Lawrence, J., Retchless A., (2010) “The myth of bacterial species and speciation”, *Biology and Philosophy 25* (4):569-588

Olson, Eric T., (1997) *The Human Animal*, Oxford: Oxford University Press

Robinson, D. (1985). “Can amoebae divide without multiplying?” *Australasian Journal of Philosophy, 63*(3), 299-319

Rose, M.R., (1991). *Evolutionary Biology of Aging*, Oxford: Oxford

University Press

Shapiro, J.A., (1998). “Thinking about Bacterial Populations as Multicellular Organisms”, *Annu. Rev. Microbiology. 52*:81-104

Spivey, E. C., Jones S. K., Rybarski J.R., Saifuddin, F.A., Finkelstein, I.J., (2017) “An aging-independent replicative lifespan in a symmetrically dividing eukaryote”, *Elife* 6, e20340

Stewart, E.J., Madden, R., Paul, G., & Taddei, F. (2005). “Aging and death in an organism that reproduces by morphologically symmetric division” *PLoS biology*, *3*(2), e45

Sober, E. (2000) *Philosophy of Biology,* Westview Press

Watve, M., Sweta, P., Prajakta, J. & Sarita, K. (2006). “Aging may be a conditional strategic choice and not an inevitable outcome for bacteria”. *Proceeding of the National Academy of Sciences.* 103 (40). 14831-14835

Wilkerson, T. E., (1995), *Natural Kinds*, Avebury, Aldershot

Wilson, E.O., Sober, E. (1989), “Reviving the superorganism”, *Journal of Theoretical Biology*. 136: 337-356

1. The term “generation” has two meanings that can be conflated, which need to be distinguished in this paper. 1) a generation can be a single reproductive event that generates an individual entity. 2) a generation can be a group of organisms that are the same number of ancestors removed from another organism, e.g. all of *X*’s great grandchildren are members of the same generation. Throughout this paper ‘generation’ has the second of these meanings unless otherwise noted. [↑](#footnote-ref-1)
2. This is not to say that philosophers and biologists don’t acknowledge that biological fission is “metaphysically interesting and mysterious” (Olson 1997, p.114). There are many metaphysical issues that actual fission cases present which are worthy of greater philosophic attention precisely because they are metaphysically mysterious. Do bacteria die during fission or do they cease to be - is there any difference between these two possibilities? [↑](#footnote-ref-2)
3. A clear example of this type of application can be seen in Robinson (1985) where his argument is framed in terms of amoebas, though its application is squarely within the metaphysics of personal identity, with little or no consideration for the biology of amoebas or asexual organisms. [↑](#footnote-ref-3)
4. Sober doesn’t actually cite the principle of the Identity of Indiscernibles, but his point has the same logical force: he says that if the parent was identified as just one of two identical offspring “we would have three objects *b, a, d,* and would find ourselves saying *b = a, b = d,* and *a ≠ d*” (Sober 2000, p.155). [↑](#footnote-ref-4)
5. The difference between biological individuals and organisms is important (cf. Queller and Strassmann, 2009 & 2014). In this context I mean to limit the consideration to individual organisms. [↑](#footnote-ref-5)
6. Throughout much of this paper I use the term ‘identity’ rather than ‘individual’ because of the logical usage ‘identity’ has in philosophy. Nevertheless, it seems there is work needed in the philosophy of biology in differentiating between biological individuality and biological identity. [↑](#footnote-ref-6)
7. O’Malley (2014) notes that the engendered language that is still used today stems from the mistaken thinking of early microbial geneticists who observed conjugation and assumed that such reproduction must be similar to eukaryotic animal sexuality. [↑](#footnote-ref-7)
8. Views of individuality that do not support such a position can be seen in, for example, Janzen (1977). According to these views genets can extend spatially through “growth” rather than “reproduction”. [↑](#footnote-ref-8)
9. Strictly speaking, if this view is accepted, then you’re no longer actually doing *phylo*genetics – rather you’re just tracing the history of a single individual. [↑](#footnote-ref-9)
10. These three ways of understanding identity have corollaries in debates over personal identity. For example, the second looks to align with Derek Parfit’s position on identity, the last on David Lewis’ four-dimensional view of identity (Rorty 1976). [↑](#footnote-ref-10)
11. If the functional immortality thesis is true. [↑](#footnote-ref-11)
12. Some argue, e.g. Shapiro (1998) & Queller and Strassmann (2009), that some *groups* of microorganisms and insect colonies might actually be better thought of as single organisms. Perhaps this model supports such views, which would mean that biologists are, in a sense, making a mistake when they say that certain single celled entities are organisms (i.e. they should be looking at the group or colony rather than the unicellular individuals). [↑](#footnote-ref-12)
13. This entails that the fission event would be asymmetrical even in a species that normally divides symmetrically. So there’s a temptation to consider the organism with the mutation the offspring. However, let’s resist that temptation. This is because it’s unclear whether the property of whatever mutation is sufficient to determine that the organism with the mutation actually is the offspring. How do you know the parent didn’t change during fission? Or one might say that the resulting organisms are asymmetrical siblings and the parent didn’t survive fission. [↑](#footnote-ref-13)
14. If A’s genetic makeup changed, through some process like LGT, we might wonder if *A* is still *A*. I’m not sure whether *A* would still be *A*, but in any case, we’re still left with an identity problem. Is genetic consistency necessary for identity? I don’t think there’s an obvious answer, thus it seems perfectly plausible to apply the immortal model even if there’s a genetic change in *A* that didn’t take place during fission. [↑](#footnote-ref-14)
15. Numerous alternatives have been proposed to construct a more accurate tree of life (O’Malley, Martin and Dupre 2010) – far too many to do justice to here. Some believe that there may be pluralistic approaches for understanding the systematics and lineages of microbes (e.g. Doolittle and Bapteste 2007, Boucher and Bapteste 2009), while others argue that traditional species concepts can’t apply to microorganisms (Lawrence and Retchless 2010). Meanwhile, metagenomics combines genetic and ecological data to shift attention away from species classification towards communities (O’Malley 2014). Whether or not a viable approach for understanding the tree of life can be developed for microorganisms, it is doubtful that the phylogenetic trees of life that are used for the world of sexually reproducing organisms can meaningfully bear on the microbial world. [↑](#footnote-ref-15)
16. Although they differ in their reproductive processes (i.e. *S. pombe* reproduces through cytokinesis, whereas *Escherichia coli* reproduces through binary fission) both have “symmetrical” offspring. [↑](#footnote-ref-16)
17. Aging is not a uniform marker of an organism in biology. Consider slime molds or *Turritopsis dohrnii*, i.e. the “immortal jellyfish”. Such organisms move back and forth between juvenile and mature stages of life while, it is believed, remaining the numerically same organism. [↑](#footnote-ref-17)
18. In 2005, Stewart, et al, presented research suggesting that the functional immortality thesis was false – seemingly functionally immortal microorganisms *do* age. Their research suggests that although unicellular organisms that reproduce symmetrically make near perfect copies of their genetic material during reproduction, resulting in organisms that are *nearly* identical, there is a functional difference between them. Thus, while the two organisms that result from fission may outwardly appear to be perfectly symmetrical there is a functional asymmetry between them due to the slower reproductive rate. The more slowly reproducing pole is identified as the older or original, parent organism. However, since Stewart et al. overturned the functional immortality thesis more research on the lifecycle of seemingly symmetrical, asexually reproducing microorganisms has taken place. The results have been conflicting (Florea 2017). Much of the research confirms Stewart’s “aging thesis”, but there is also a growing body of evidence that runs counter to the aging thesis and aligns with the traditional “immortal” view. Some species of microorganisms appear to propagate with perfect symmetry when presented with favorable conditions, like *E. coli* and the fission yeast *S. pombe* (Coelho, Dereli, Haese, et al. 2013 & Spivey et al. 2017). Coelho et. al note that *S. pombe* continues to reproduce at the same rate as long as it is presented with a favorable environment. If *S. pombe* is not presented with any stressors, it reproduces with seemingly prefect symmetry, with no decline in fitness, leading some researchers to believe the species is functionally immortal. [↑](#footnote-ref-18)
19. Consider Davidson’s swamp man (1987), Sober’s Martian tiger (2000) or Wilkerson’s (1995) gorillas and humans. [↑](#footnote-ref-19)
20. Whether you think a slowed reproductive rate is sufficient for aging is a serious and interesting biological question. There are competing accounts of whether cell aging is programmed or mechanistic (cf. Florea 2017). [↑](#footnote-ref-20)