The evolution of life cycles with haploid and diploid phases

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Summary

Sexual eukaryotic organisms are characterized by an alternation between haploid and diploid phases. In vascular plants and animals, somatic growth and development occur primarily in the diploid phase, with the haploid phase reduced to the gametic cells. In many other eukaryotes, however, growth and development occur in both phases, with substantial variability among organisms in the length of each phase of the life cycle. A number of theoretical models and experimental studies have shed light on factors that may influence life cycle evolution, yet we remain far from a complete understanding of the diversity of life cycles observed in nature. In this paper we review the current state of knowledge in this field, and touch upon the many questions that remain unanswered. *BioEssays* **20**:453–462, 1998.   © 1998 John Wiley & Sons, Inc.

Introduction

In 1851, Hofmeister[1] recognized that plants alternate between two distinct phases, yet it was not until 1894 that Strasburger[2] proposed that this "alternation of generations" represented an alternation between haploid and diploid phases.[3] Such an alternation of generations is a necessary consequence of sexual reproduction, since a haploid phase must follow meiosis and a diploid phase must follow gamete fusion, but the lengths of these two phases vary widely among organisms.[4] This variability is especially pronounced among such organisms as algae and protists, which have life cycles ranging from complete haploid development to complete diploid development, as illustrated in Figure 1.

During the past 20 years, there has been a resurgence of interest in the evolution of life cycles and ploidy levels. However, much of both the theoretical[4–15] and experimental[16–18] work has concentrated on how and why diploidy has evolved as the dominant state in "higher" plants and animals (reviewed in ref. 19). This focus on the advantages of diploidy has tended to hinder our understanding of the diversity of life cycles seen among organisms and in some cases has

resulted in erroneous interpretations of comparative patterns (as argued in ref. 20). Recently, the focus has shifted toward a somewhat more interesting question: why do many eukaryotes (e.g., many protozoa, algae, fungi, mosses, and ferns) maintain an alternation of generations in which there is substantial development in both haploid and diploid phases? This shift has led to a number of theoretical predictions about when we might expect to see the evolution of haplonty (somatic development only in the haploid phase), diplonty (somatic development only in the diploid phase), or haploid-diploidy (somatic development in both phases). The purpose of this review is to outline the type of variation in life cycles that exists among eukaryotes, summarize theoretical and experimental studies of life cycle evolution, and suggest directions for future research.

Life cycle variation among eukaryotes

The fact that nearly all metazoan taxa undergo somatic development as diploids has strongly shaped our perception of life cycles, leading to a belief in the inherent superiority of the diploid state. One notable exception to complete diplonty is the occurrence of arrhenotokous animal species, in which haploid males are produced parthenogenetically by diploid females, which are themselves produced sexually (Table 1). Among zoologists, the term "haplo-diploid" is usually reserved to describe taxa with haploid males and diploid females, and so we will use "haploid–diploid" to refer to organisms that alternate between independent haploid and

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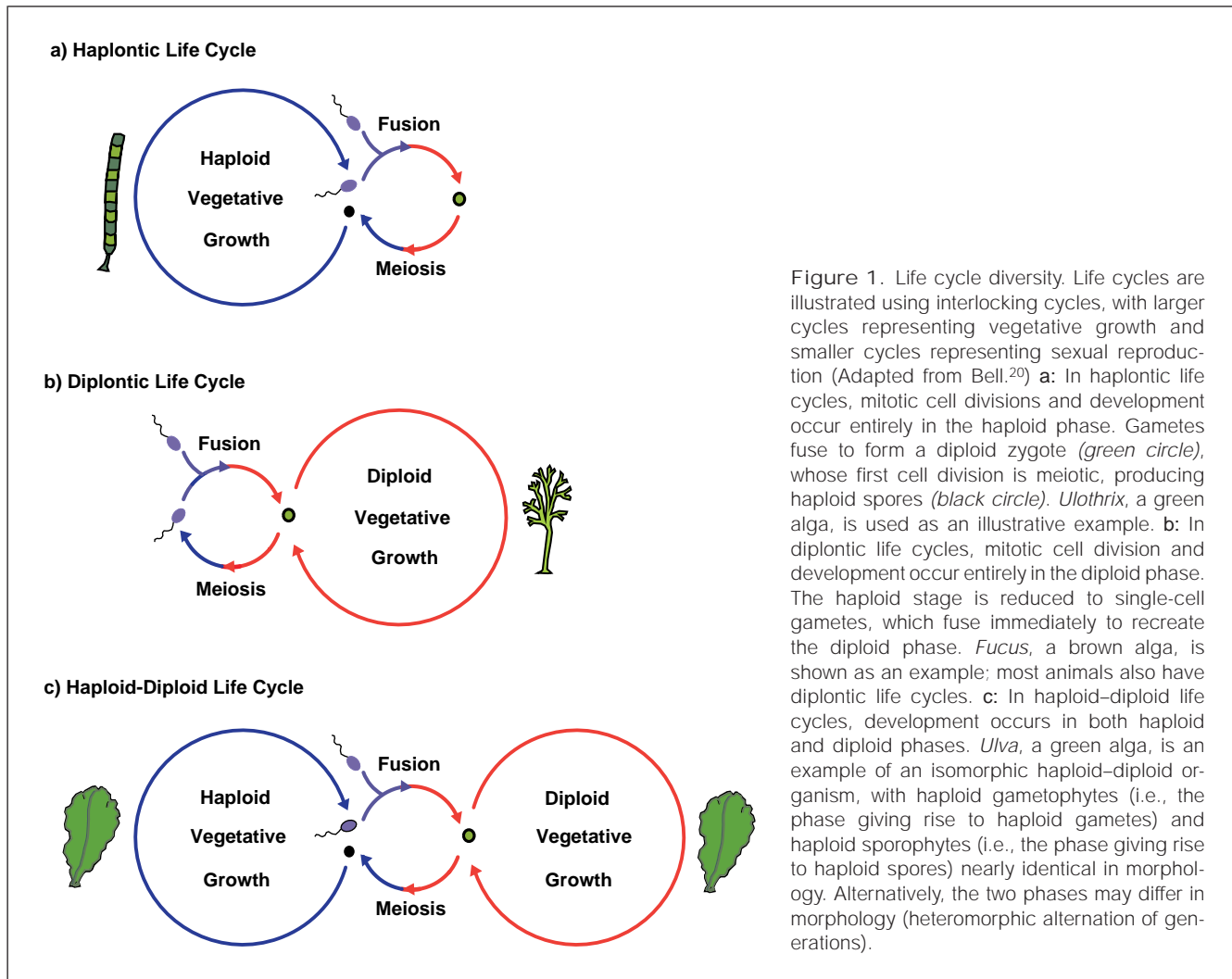
Figure 1. Life cycle diversity. Life cycles are illustrated using interlocking cycles, with larger cycles representing vegetative growth and smaller cycles representing sexual reproduction (Adapted from Bell.[20]) **a:** In haplontic life cycles, mitotic cell divisions and development occur entirely in the haploid phase. Gametes fuse to form a diploid zygote *(green circle)*, whose first cell division is meiotic, producing haploid spores *(black circle). Ulothrix*, a green alga, is used as an illustrative example. **b:** In diplontic life cycles, mitotic cell division and development occur entirely in the diploid phase. The haploid stage is reduced to single-cell gametes, which fuse immediately to recreate the diploid phase. *Fucus*, a brown alga, is shown as an example; most animals also have diplontic life cycles. **c:** In haploid–diploid life cycles, development occurs in both haploid and diploid phases. *Ulva*, a green alga, is an example of an isomorphic haploid–diploid organism, with haploid gametophytes (i.e., the phase giving rise to haploid gametes) and haploid sporophytes (i.e., the phase giving rise to haploid spores) nearly identical in morphology. Alternatively, the two phases may differ in morphology (heteromorphic alternation of generations).

diploid phases in their life cycle. This latter type of alternation is unknown among animals but is prevalent in other eukaryotes.

In plants, the traditional view (Fig. 2) is that evolution has proceeded through a steady reduction in the extent of the haploid phase and an increasing dominance of the diploid phase.[5] This view has also reinforced the presumption that diploidy is evolutionarily favored, with the underlying implication that predominantly haploid organisms are evolutionary relics. There are a number of reasons to doubt such a conclusion, however, which become apparent upon examination of ploidy evolution in groups where life cycles are more variable.

Life cycles with both haploid and diploid phases are widespread in red algae, most brown algae, many green algae, some fungi, foraminiferans, mosses, and ferns.[4,21] The two phases in these organisms vary from extreme heteromor-

phy (large differences in morphology) to isomorphy (nearly identical in morphology). The persistence of both phases among a diversity of organisms suggests that haploid–diploidy is a remarkably stable, rather than a transitional, state in these groups (reviewed in ref. 22). While completely diplont species exist in many of these taxa, they have not led to the competitive elimination of other life cycles. Of even greater interest is evidence that several taxa have, over evolutionary time, developed an expanded haploid phase and a shortened diploid phase. These include species of green algae,[23] brown algae,[24] and yeast.[25] The evolution of an increased haploid phase is completely unexpected under the traditional view that diploidy is evolutionarily favored, and it demands that we determine the conditions that favor increased haploidy. In the following sections, we review some of the main advantages that have been proposed for different life cycles.

TABLE 1. Incidence of Haplo-Diploidy in Animals*

Taxa	Comments
Arrhenotoky	
Monogonont rotifers (Monogononta: Rotifera)[31,65]	Characteristic of order[a]
Pinworms (Oxyurida: Nematoda)[66]	Characteristic of order[a]
Mites (Acarina: Arachnida)[67]	Independently arisen multiple times[b]
Thrips (Thysanoptera: Insecta)[68]	Characteristic of order[a]
Iceryine scale insects (Margarodidae: Coccoidea: Homoptera: Insecta)[69]	Found in five genera
Soft scale insects (Coccidae: Coccoidea: Homoptera: Insecta)[69]	Known in four species[c]
Whiteflies (Aleyrodidae: Homoptera: Insecta)[70]	Characteristic of family[a]
Micromalthid beetles (Micromalthidae: Coleoptera: Insecta)[68]	Found in the one species of the family
Bark beetles (Scolytidae: Coleoptera: Insecta)[71]	Found (independently?) in *Dryocoetini* and *Xyleborini*
Ants, bees, wasps, sawflies (Hymenoptera: Insecta)[68]	Characteristic of order[a]
Pseudo-arrhenotoky	
Mites (Ascoidea: Acarina: Arachnida)[67]	Known in two families
Armored scale insects (Diaspodidae: Coccoidea: Homoptera: Insecta)[69]	Known in multiple groups[d]
Lecanoid scale insects (Coccoidea: Homoptera: Insecta)[69]	Known in 10 families[e]
Bark beetles (Scolytidae: Coleoptera: Insecta)[72]	Found in *Hypothenemus*
Gall midges (Cecidomyidae: Diptera: Insecta)[65]	Known in three genera[f]

*Arrhenotoky (haploid males develop from unfertilized eggs) has originated about 17 times. Pseudo-arrhenotoky (males develop from diploid fertilized eggs but subsequently eliminate or silence the paternal genome) has also evolved numerous times.
[a]With the exception of female-only (thelytokous) taxa.
[b]Norton et al.[67] argue that arrhenotoky has arisen eight times within mites. This may be an underestimate, as many groups have not been adequately studied.
[c]In the Coccidae, males develop from unfertilized haploid eggs.[69] The first two cleavage nuclei fuse, however, to form a homozygous diploid individual. One of the haploid genomes subsequently becomes heterochromatic (with tightly packed and generally unexpressed DNA), a common phenomenon in male coccids.
[d]In the Diaspididae, males develop from fertilized diploid eggs.[69] The paternal genome is excluded from the developing embryo, such that most of the soma and the germline are haploid. This form of haplo-diploidy is thought to have arisen multiple times within the coccids.
[e]In the lecanoid and *Comstockiella* systems, the paternal genome becomes heterochromatic and is unexpressed in most somatic tissues.[69] In addition, the paternal genome is either lost before prophase I or is not packaged into sperm.
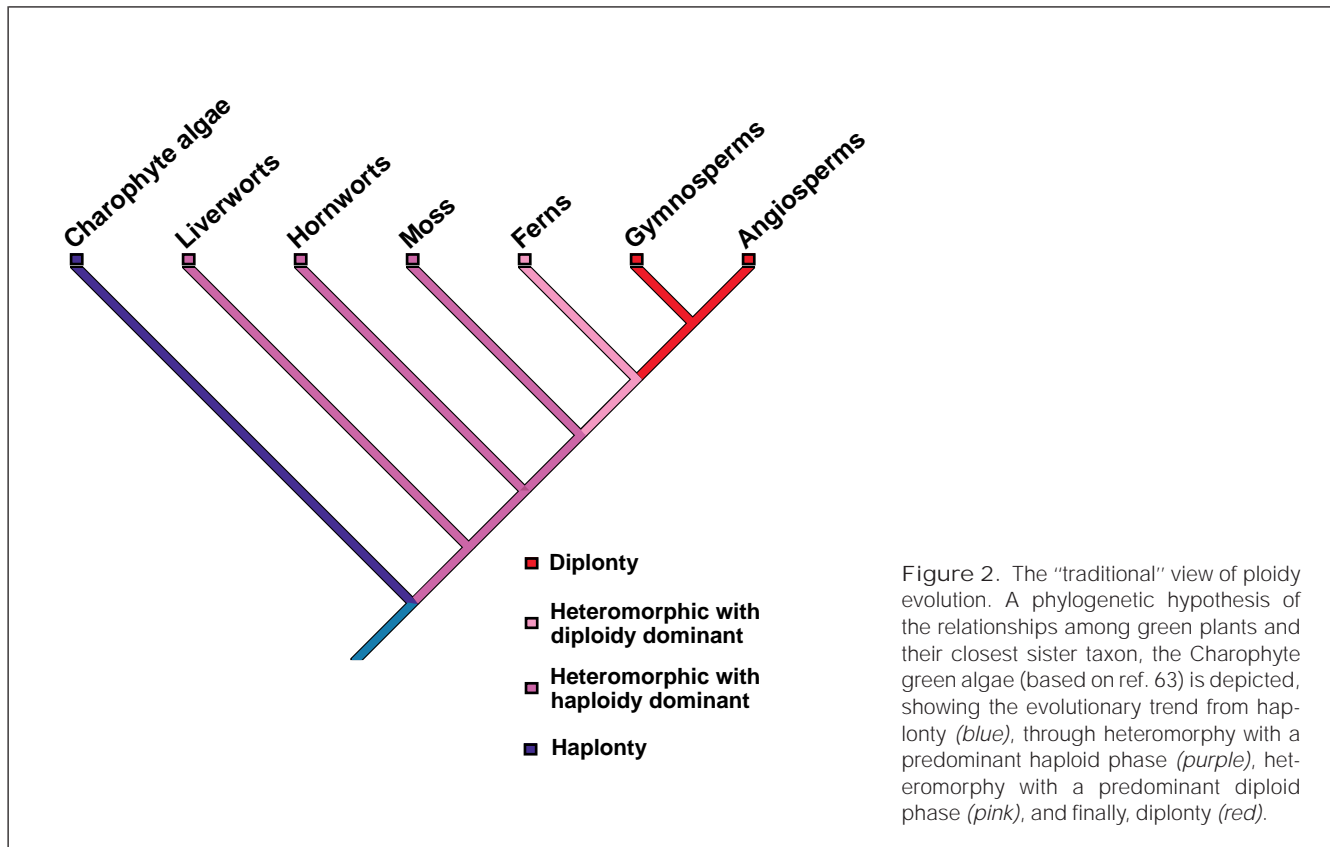[f]Paternal genome loss during male meiosis is also known in a related family of fungus gnats (Sciaridae). In the Cecidomyid species *Heteropeza pygmaea*, some eggs (those produced by the winged adult form) develop into females bearing only a haploid set of chromosomes in the soma, representing, as far as we are aware, the only regular instance of female haploidy in animals.[65]

Advantages of diploidy

One of the strongest genetic consequences of being a sexual diploid is that nearly all deleterious mutations within the genome are masked. This follows from the empirical observation that the vast majority of mutations that adversely affect fitness are partially recessive.[26] Since deleterious mutant alleles are generally rare within a population, it is unlikely that a diploid produced by random mating will carry two mutant copies of an allele at a locus. By contrast, haploids express each and every mutation within their genome. Consequently, mutant individuals with a prolonged diploid phase should have a higher fitness, and diploidy should be selectively favored.[14,27] A related benefit of diploidy may be in the masking of mutations that occur in somatic cells during development or as a result of cell turnover. Such masking is thought to be necessary for the survival of large multicellular organisms in which numerous cell divisions occur.[27–30] Protection against somatic mutations in diploids cannot explain why diploidy is advantageous in organisms that have endopolyploidy among their cells. For example, in some red algae, most of the cells of both isomorphic haploid and diploid phases are polyploid or multinucleate, so buffering of somatic mutations should occur in all cells.[7]

Having two copies of each gene may also hasten the rate of adaptation of diploid organisms to new environments. Not only do diploids harbor twice as many genes capable of beneficial mutation,[17] but, since diploids mask deleterious mutations, there also tends to be a larger pool of mutant alleles within predominantly diploid populations. This pool provides a source of genetic variability that may prove to be beneficial in the face of environmental change.[31] Similarly, the acquisition of new functions may be faster in diploids because the "extra" gene copy can preserve mutant alleles that serve a new purpose, while in haploids gene duplication must predate the evolution of novel functions.[32]

Figure 2. The "traditional" view of ploidy evolution. A phylogenetic hypothesis of the relationships among green plants and their closest sister taxon, the Charophyte green algae (based on ref. 63) is depicted, showing the evolutionary trend from haplonty *(blue)*, through heteromorphy with a predominant haploid phase *(purple)*, heteromorphy with a predominant diploid phase *(pink)*, and finally, diplonty *(red)*.
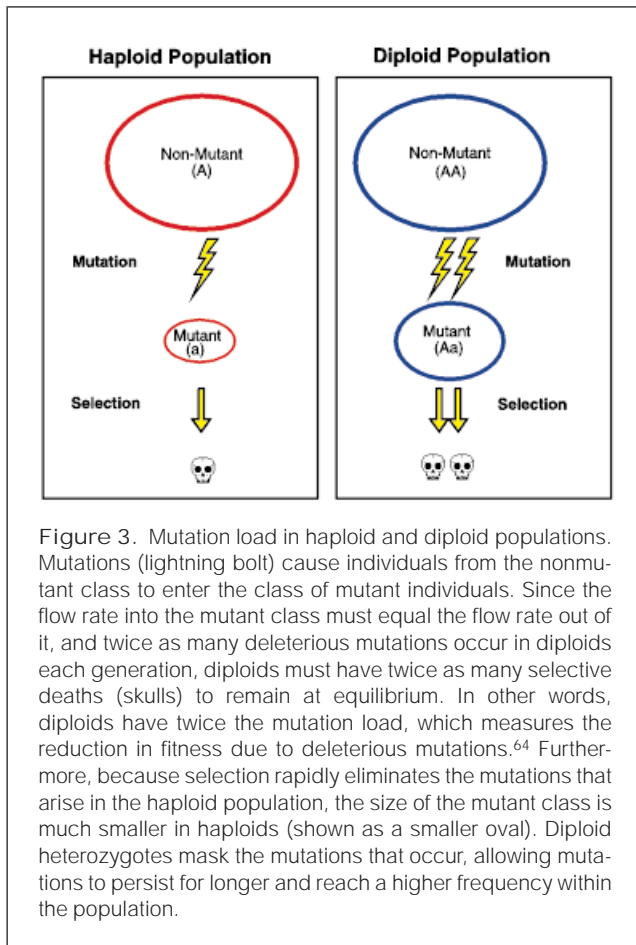
Advantages of haploidy

Recent theoretical work on life cycle evolution has demonstrated that the above-mentioned advantages to diploidy can, under certain circumstances, work against them. Masking in diploids, for example, is a double-edged sword: it is beneficial to the individual (who survives) but is disadvantageous to the offspring (who inherit more deleterious mutations from their parents). In fact, because mutations are more efficiently eliminated in haploids,[33] haploid populations tend to carry fewer mutations and have a higher average fitness at equilibrium than diploid populations[27] (Fig. 3). Even within a population, an individual that arises with a longer haploid phase will be more likely to die, but if it survives it will carry, on average, fewer mutations. Its offspring will hence carry fewer mutations and, in future generations, any new mutations that occur will be exposed to selection unmasked in the haploid phase. Because selection is more efficient at eliminating deleterious mutations from haploids, a longer haploid phase can be favored by evolution under certain circumstances. There is, however, an important caveat to the spread of haploidy within a population: the advantages of a longer haploid phase must be confined, to some extent, to individuals with a longer haploid phase. If there is a high degree of genetic mixing within a population, the advantages of haploidy (fewer mutations) will be shared with the more diploid members of the population, who then gain both the advantages of fewer mutations and of masking. Consequently, theoretical models of this phenomenon have led to the conclusion that predominantly haploid life cycles are favored if (1) sex is rare, (2) recombination is rare, (3) selfing is common, or (4) assortative mating is common.[13,23,34,35]

In a similar manner, if there is selection among cells within an individual, masking of somatic mutations may actually favor haploid over diploid life cycles. Somatic mutations in haploid individuals would be eliminated rapidly by cell-lineage selection but would be masked and would persist in a developing diploid individual. Models that include cell-lineage selection predict that multicellular organisms that are relatively undifferentiated and therefore have a greater opportunity for selection among cells will more likely evolve haploid life cycles than will multicellular organisms with highly differentiated tissues in which cell-lineage selection is limited.[36]

What about the hypothesis that diploids evolve faster? While it is true that a diploid individual is twice as likely to carry a new beneficial mutation, the fitness benefits of mutations will be masked to some extent by the alternative allele. The frequency of a beneficial mutation will therefore rise less rapidly within a diploid population and the mutation will be more susceptible to loss while rare. Consequently, diploids

Figure 3. Mutation load in haploid and diploid populations. Mutations (lightning bolt) cause individuals from the nonmutant class to enter the class of mutant individuals. Since the flow rate into the mutant class must equal the flow rate out of it, and twice as many deleterious mutations occur in diploids each generation, diploids must have twice as many selective deaths (skulls) to remain at equilibrium. In other words, diploids have twice the mutation load, which measures the reduction in fitness due to deleterious mutations.[64] Furthermore, because selection rapidly eliminates the mutations that arise in the haploid population, the size of the mutant class is much smaller in haploids (shown as a smaller oval). Diploid heterozygotes mask the mutations that occur, allowing mutations to persist for longer and reach a higher frequency within the population.

quires a large portion of the energy budget of a dividing cell,[11] a cost that would be halved in haploid cells.

Cavalier-Smith[38] proposed a slightly more general version of this hypothesis, suggesting that ploidy evolution might be a byproduct of selection for optimal nuclear or cell size. Since diploid nuclei and cells tend to have larger volumes than haploid ones, conditions that favor large size might select for higher ploidy levels, while conditions favorable to smaller individuals will select for haploid life cycles. He suggested that observed variation in DNA content among protists (and the related variation in cell size) results primarily from variability in the selective pressures acting on a population. For example, in large predatory protozoans (e.g., amoebae, foraminiferans, ciliates) diploidy dominates, whereas in small endoparasites (e.g., sporozoa), haploidy is more prevalent. Similarly, r-selection, which favors rapidly growing organisms, may favor smaller haploid cells, while K-selection may favor larger diploid cells that are more competitive under dense conditions. However, the r- and K- selection hypothesis does not fit successional patterns seen in algae and assumes that "simple" organisms showing haploidy are all strongly r-selected.[11] In addition, DNA is metabolically and ecologically expensive, so one would expect that easier ways of regulating cell size might exist.[11]

Advantages of haploid–diploidy

Each of the genetic hypotheses discussed above can be shown to favor haploidy under some conditions and diploidy under others. It is reasonable to expect that these selective forces may occasionally balance, favoring life cycles with both an extended haploid phase and an extended diploid phase. Unfortunately, this has not proved to be the case. None of the previous genetic models predicts maintenance of both phases: evolution eventually favors either diplonty or haplonty. The hypotheses that do successfully predict the maintenance of both phases posit some form of intrinsic advantage to haploid–diploidy.

One potential advantage of haploid–diploidy is an increased opportunity to exploit resources. For instance, in the presence of disruptive selection favoring two distinct phenotypes, a species may evolve a heteromorphic life cycle with the haploid and diploid phases occupying different ecological niches.[39,40] There are, however, other mechanisms that do not depend on ploidy by which a species may evolve multiple morphs. For example, the frequent occurrence of sporophytes developing from haploid rather than diploid cells in brown algae demonstrates that morphological state may be regulated by environmental factors, such as daylength, or by developmental history, rather than by ploidy level.[24] The argument is simply that it may be easier to evolve divergent morphologies starting from different ploidy phases, either because it is easier to evolve differential gene expression or

will evolve faster and diploid life cycles will be favored over haploid life cycles only if beneficial mutations tend to be dominant (although there is no clear evidence concerning this point) and if genetic mixing is frequent within the population.[12,37] Another factor is that diploids maintain more standing genetic variation because deleterious mutations persist longer in the population when masked, which may also improve the ability of diploids to respond to changing environments. This suggestion is more difficult to evaluate in the absence of empirical data. Specifically, it is unknown to what extent previously deleterious mutations are beneficial after environmental change.

Other advantages of haploidy have been posited. Lewis[11] proposed that haploid cells may often have a nutritional advantage over diploid cells, especially in unicellular organisms. Haploid cells are often smaller than diploid cells[15,38] and thus have a higher surface area to volume ratio. Since the ability to transport nutrients across the cell membrane depends on surface area, this increased ratio may lead to improved growth rate or survival, especially under nutrient limited conditions. Furthermore, DNA replication often re-

because there are inherent morphological differences that may be amplified by selection.

A similar argument is that haploid–diploidy allows for two different modes of dispersal of genetic material: via haploid gametes and/or diploid zygotes produced by the haploid gametophyte generation and via haploid spores produced by the diploid sporophyte generation. Certainly, haploid gametes must be released in the vicinity of other gametes, which will place different selective constraints on gametophytes and sporophytes.[24] Futhermore, haploid spores often have higher dispersal abilities, whereas diploid spores tend to have higher survivorship.[41] This may result in a best-of-both-worlds reproductive strategy,[42,43] where diploid spores expand in established populations and haploid spores colonize new sites.[41] However, dichotomous dispersal strategies may not require ploidy differences. For example, there may be differences in dispersal between male and female gametes. In the red alga, *Gracilaria verrucosa*, both haploid and diploid spores survive for longer than male gametes and thus have more opportunities for dispersal, and it is actually the haploid spores that have the longest survival.[41]

Another potential advantage of haploid–diploidy is that sex occurs half as often, assuming that individual generation times are the same length as in haplont or diplont organisms.[44] This is illustrated in Figure 1, where for every sexual cycle (small circles) there is only one vegetative cycle in haplonts and diplonts, but two in haploid–diploid cycles. Biphasic life cycles may therefore halve the costs of sex (e.g., producing male gametes and ensuring fertilization with a compatible individual). If this is true, one would predict that haploid–diploidy would be favored under conditions in which the costs of sex are high (especially in sparsely populated areas), although one might reasonably expect that asexual reproduction would evolve instead under such conditions.

Kondrashov[73] suggested that ploidy cycles (i.e., alternation between high and low ploidy levels), which may be found in organisms with or without sexual reproduction, may act to reduce the mutation load compared with permanently diploid or polyploid states. In this way, the beneficial effects of masking provided by additional gene copies in the higher ploidy state may be enjoyed while still retaining the capacity to reduce the burden of deleterious mutations in the lower ploidy state.

Many more possibilities remain to be explored. In particular, models need to be developed that allow for changing environments over time or space. Such models may be much more favorable to the maintenance of both haploid and diploid phases and may provide specific predictions about the distribution of such life cycles.

Empirical evidence

We have described only a small fraction of the hypotheses that have been put forward to explain the evolution of different life cycles (see also refs. 18, 19, 20, 22, 24, 31). Despite the plethora of hypotheses, few experimental tests have been conducted. The richest source of available information comes from comparative analyses among species. Such analyses are often hampered by a lack of detailed information about the phylogenetic relationships among species, their modes of reproduction, and the selective forces acting on haploid and diploid individuals in nature. Experimental tests raise their own difficulties; for example, it is often difficult to culture organisms with complex life cycles and conclusions are often clouded by problems with culture techniques (e.g., selection within a chemostat). Furthermore, mutations that affect ploidy levels often have confounding effects on the frequency of sex. Another problem is that any search for advantages of one ploidy level over the other will be inherently biased when the organisms examined have been evolutionarily preadapted to exist in one form or the other (shown elegantly by V. Perrot, personal communication). Here we outline some of the evidence that does exist concerning life cycle evolution.

Comparative analyses

Bell[31] collected much of the known information about life cycle variants in so-called "lower" eukaryotes (i.e., algae and protozoans) in order to evaluate hypotheses on life cycle evolution. We extracted information from his Table 5.7 to show how life cycles vary with degree of sexuality and size/complexity of the vegetative phase, as shown in Figure 4. Unfortunately, no clear pattern emerges across orders of protists (Fig. 4a). Diploids tend to be either unicellular (diatoms, flagellates, and ciliates) or multicellular with cellular specialization (dinoflagellates), but this may be a phylogenetic constraint rather than an adaptive strategy. Haploids are found in all regions of this "life cycle space," regardless of taxonomic grouping. Among families within the green algae (class Chlorophyceae, Fig. 4b) a trend toward increasing diploidy with complexity becomes apparent. There does not, however, appear to be a correlation between degree of sexuality and ploidy level. Similar results were found in brown algae by Bell:[24] no apparent relationship was observed between dominant ploidy level and the ability to either self or reproduce asexually via haploid sporophytes.

These comparative analyses suggest that there may not be a correlation between the extent of genetic mixing within a population and its life cycle. This conclusion is extremely tentative, as it is based on only crude measures of the extent of random mating within a population and may be phylogenetically biased. Evaluation of genetic data concerning the degree of inbreeding and the extent of genetic associations among loci would provide a greatly improved measure of genetic mixing within a population. If the lack of correlation is upheld by better data, however, we must conclude that deleterious mutations have not played an important role in the evolution of life cycles of lower eukaryotes. Otherwise, the

masking of deleterious mutations in predominantly sexual populations would favor diploidy, while the purging of deleterious mutations in less sexual populations would favor haploidy. The somatic protection hypothesis fares better. As shown in Figure 4b, the diploid phase is more common among multicellular chlorophytes, consistent with the idea that diploids provide increased protection against somatic mutations in large organisms. This hypothesis, however, is not supported at higher taxonomic levels (Fig. 4a) and fails to explain the existence of multicellular haploid phases.

Experimental data

The hypothesis that has received the greatest amount of experimental attention has been Lewis's nutrient limitation hypothesis. Adams and Hansche[16] compared growth rates in asexual haploid and diploid strains of *Saccharomyces cerevisiae* maintained in a chemostat. In contrast to the widely held belief among yeast researchers that diploids always tend to outgrow haploids,[25,45] these investigators concluded that, under nutrient rich conditions, diploids were just "double haploids" and did not have an intrinsic growth advantage compared with haploids. In support of the nutrient limitation hypothesis, they also found that when growth in the chemostat was limited by organic phosphate availability, haploid cells grew more rapidly than diploids. However, this was not found for dextrose or inorganic carbon limitation, where there was no significant difference in growth of diploids or haploids. Similarly, using "quasi-continuous" cultivation of haploid and diploid *S. cerevisiae,* Glazunov et al.[46] found that diploids outcompeted haploids in rich medium, while haploid cells had an advantage in minimal medium and in the presence of a competitor (the yeast, *Pichia pinus*). It was later reported,[47] however, that diploids completely displaced haploids in rich and minimal medium, and in the presence of the *Pichia pinus* competitor. These contradictory results emphasize that conclusions on ploidal dominance may be influenced significantly by the particular environmental and experimental conditions used.

In multicellular organisms, the applicability of the nutrient limitation hypothesis is less clear, since both haploid and diploid individuals may grow to the same size despite differences in nuclear and cell size. Nevertheless, in an experiment comparing growth rates of juvenile isomorphic haploid and diploid phases of the red alga, *Gracilaria verrucosa*, Destombe et al.[48] found support for the nutrient limitation hypothesis: haploids had a growth advantage in nonsupplemented sea water (i.e., nutrient poor conditions) while diploids had an advantage in supplemented sea water. By contrast, Littler and Littler[49] found no significant differences in net photosynthesis or calorific content among ploidy levels of the isomorphic red alga, *Polcavernosa debilis*.
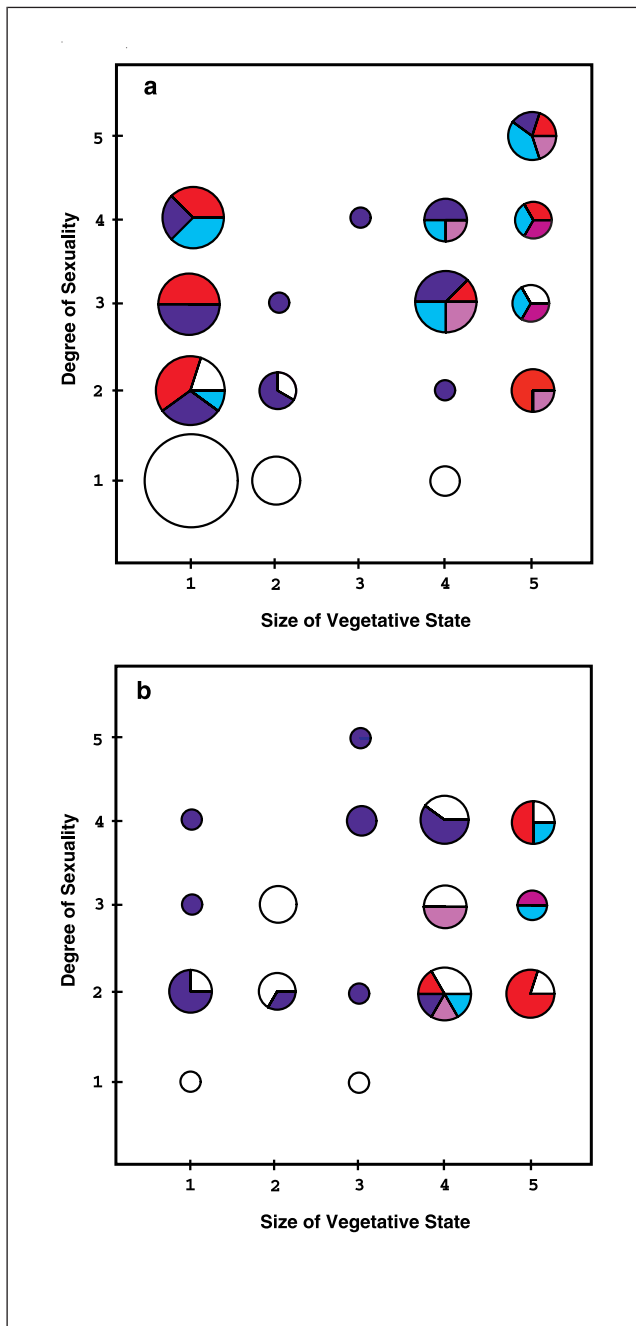
Figure 4. Life cycle variation. The frequency of organisms showing haploid *(purple)*, diploid *(red)*, heteromorphic *(turquoise)*, and isomorphic *(light purple)*, and unknown life cycles *(open)* are plotted with respect to the degree of sexuality (1 = obligately asexual; 5 = obligately sexual) and size/complexity of the vegetative phase (1 = unicellular; 2 = 2 − 100 cells in colony; 3 = 100 − 1,000 cells in colony; 4 = macroscopic colonies to 1 cm; 5 = macroscopic, several cells thick). The data were extracted from Table 5.7 of Bell.[31] Circle areas are proportional to the number of taxa showing a particular combination of traits, with the smallest circles representing single taxa. **a:** Variation among orders of protists. No correlation is apparent between life cycle and either degree of sexuality or complexity. **b:** Variation among families within the class Chlorophyceae (green algae). Increased diploidy is observed with increased complexity but not with increased sexuality.

The relevance of historical ploidy levels to the fitness of haploid and diploid yeast was examined by V. Perrot (personal communication) using *S. cerevisiae*, which is normally diploid, and *Schizosaccharomyces pombe*, which is normally haploid. Yeast were grown in liquid culture and then competed on solid medium. She found that diploid *S. cerevisiae* had an overall advantage over haploid *S. cerevisiae* under both rich and poor media conditions, while haploid *S. pombe* had an overall competitive advantage over diploid *S. pombe*. She concluded that the ploidy history of the species and not nutrient conditions may be the most important factor determining the outcome of competition experiments in the laboratory. This was also suggested for a normally haploid multicellular organism, *Aspergillus niger*, for which haploids outcompeted diploids after only a few generations, indicating that any potential advantage of diploidy was not sufficient to overcome the advantages of having adapted previously to haploidy.[18]

In another experiment with *S. cerevisiae*, Paquin and Adams[17] evaluated the hypothesis that the rate of adaptation to new environments is faster in diploids than in haploids because of an increased beneficial mutation rate. These investigators looked for evidence of adaptive mutations sweeping through populations of yeast grown in a chemostat. By tracking changes in the frequency of a marker genotype, they inferred that diploids fixed more adaptive mutations than haploids, with mutations in diploids causing approximately the same fitness increment as mutations in haploids. The observed fitness benefits were not, however, large enough to account for the fixation of so many mutant alleles in so little time,[37,50] suggesting that not all the mutations were fixed. In addition, fitnesses at the end of the experiment were equal to or lower than those at the beginning of the experiment.

These experimental studies are tantalizing but leave open many unresolved questions. In particular, exactly how much of an advantage does masking deleterious mutations provide? How important are somatic mutations to fitness and how do haploid and diploid multicellular organisms cope with such mutations? What are the conditions that change the outcome of competition experiments from lab to lab? Further experimentation is necessary to resolve these issues.

Is ploidy evolution a one-way street?

Thus far, we have focused on factors that may be important in the evolution of life cycles assuming that the potential for life cycle variability exists within the species. It may be, however, that some taxonomic groups are less likely to give rise to life cycle variants. Bell[20] suggested that, when there is a great disparity in the potential for growth of haploid and diploid individuals, this disparity characterizes all members of a phylum (e.g., all charophytes are haplontic; all chordates are diplontic), whereas in taxa in which development can occur in both haploid and diploid individuals, life cycles vary widely (e.g., chlorophytes, phaeophytes, rhodophytes). That is, once a certain ploidy level has become dominant within a taxonomic group, it may be difficult to expand the alternate ploidy phase, either because the necessary mutations simply do not arise or because individuals with atypical ploidy levels are unable to develop normally.

If, for example, the diploid phase is dominant and every individual carries a large number of deleterious mutations, then haploid individuals that appear simply may not be able to survive even one generation with unmasked mutations. This is not very plausible in sexual protists and plants where survival in the haploid stage is a necessary part of the life cycle. Another possibility is that, after a long history of diplonty (or haplonty), an organism may evolve developmental pathways that depend on having the appropriate ploidy level. For example, haploid mutants may be negatively affected by the halving of gene expression for certain proteins, especially in the early stages of development, when a complex system of induction and cell-cell interactions mediate the successful production of a normal individual.[52] In support of this view, haploidy has long been known to cause developmental abnormalities in animals.[51,52] Similarly, new diploids might initially be presented with problems associated with overexpression of certain key protein products that must be compensated for by mechanisms to reduce redundant or excessive gene expression. Polyploid taxa are known to reduce the amount of duplicate gene expression after the initial polyploidization event (e.g., ref. 54), suggesting that there is a cost to maintaining production of "extra" proteins. Such phenomena as X-inactivation and genomic imprinting in diploid organisms could reflect the necessity for maintaining haploid levels of expression at key developmental stages.

Multiple origins of haplo-diploidy in a variety of invertebrate taxa (Table 1) prove that it is not impossible to be a haploid animal.[44] Nevertheless, vegetative haploidy has never fully evolved in both sexes in multicellular animals,[31] and the relatively restricted distribution of arrhenotoky leaves open the possibility that, for the vast majority of animals, a haploid phase is no longer a possibility. Similarly, in seed plants, the haploid phase is entirely dependent on the diploid phase for nutrition and for appropriate regulatory signals. In such cases, it may prove impossible for the haploid phase to exist as an independent entity (reviewed in ref. 55).

Conclusions and future directions

"For greater changes the chance of improvement diminishes progressively, becoming zero, or at least negligible, for changes of a sufficiently pronounced character."[56]

Of all the genetic changes that are possible within the genome, changes in ploidy level would appear to be the most drastic and least likely to produce a functioning organism. As

Fisher argued by analogy, while it might be possible to improve the focus of a microscope lens by small adjustments, large adjustments almost surely degrade an image. It is, therefore, a rather surprising finding that gross changes in genome size are commonplace,[57] with chromosome number and ploidy levels changing frequently over evolutionary time (e.g., *Xenopus*).[58] Moreover, a large fraction of species on earth are capable of survival in both a haploid and a diploid form. Thus, it is necessary to question the assumption that changes in genome copy number are, by necessity, drastic changes. During every mitotic cell cycle, the genome doubles and halves, and all cells must be tolerant of the subsequent changes in gene dosage. Furthermore, development clearly can proceed in a manner that depends little on the ploidy level of the individual, as demonstrated by organisms with an isomorphic alternation of generations, such as *Ulva* and *Gracilaria*. Changes in the number of genomes simply do not necessitate drastic changes in morphology.

The large degree of variation seen among groups in the duration of haploid and diploid phases suggests that life cycle strategy can be viewed as a selectively variable trait capable of continued evolutionary modification.[59] For example, yeast such as *Saccharomyces rouxii* and *Hansenula wingei* show rapid oscillations between haploid and diploid phases,[25] in contrast to species such as *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe,* which exist predominantly in one state or the other. Among algae, closely related taxa can exhibit widely variant life cycles, and a single species can exhibit differences in its life cycle across various temporal and spatial scales.[22] The causes of cycle variability are only poorly known, but in some cases may have a genetic[60] or an environmental basis.[61]

Despite the very limited number of experimental studies that have addressed these questions, recent theoretical work has posed more definite questions for future experimental research. Generation of more specific predictions provides us with greater power to detect which hypotheses may or may not have played a major role in ploidy evolution. For instance, the masking hypothesis does not appear to be consistent with ploidy evolution in the algal groups examined; the nutrient limitation hypothesis has been supported under certain conditions in algae and yeast, but differences in nutrient uptake may be a consequence of historical ploidy levels rather than a driving or maintaining force in life cycle evolution; the cell size optimization hypothesis is only supported in certain cases. The major contribution of the more recent theoretical studies is their focus on life cycle diversity (especially the maintenance of haploid and diploid phases) rather than on evolution toward diploidy. The studies conducted by Destombe et al.[41,48,62] comparing the abundance and attributes of haploid and diploid phases of algal life cycles are some of the few that describe the parameters critical to these models. More such carefully controlled studies are required before a clear picture is gained of how and why haploid and diploid life cycles have evolved and are maintained. Organisms for which the effects of ploidy can be removed at least partially from the effects of sexual reproduction and for which life cycles can be manipulated (e.g., yeast, some algae) are the most useful candidates for experimentation. One exciting area that has recently begun to receive attention is the effect of ploidy changes at the molecular level.[74] With the recent completion of the yeast genome project and the ever expanding database on sequences from other organisms, the potential to examine both ecological and molecular consequences of life cycle evolution should now be a feasible goal.

Currently we cannot definitively answer the question: Why do many eukaryotes maintain an alternation of generations in which there is substantial development in both haploid and diploid phases? However, through the continued interaction of theoretical and empirical studies, we will undoubtedly gain insight into this important evolutionary phenomenon.

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