Narrow Roads to Fern Land: reanalysing the paradox of sex

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Abstract. Following some major thought on the evolutionary maintenance of sex leads to a new hypothesis about the role of life cycles. Organisms with a heterogonic life cycle, like strawberries, propagate contrary to what would be adaptive under red-queen selection from micro-parasites. Their recombinant offspring disperses, but their clonal offspring stays close to the parent. In diplohaplontic organisms, like ferns, fertilisation and meiosis occur in different generations. Recombination is spread over the whole life cycle. Their zygotes grow on the spot of their maternal gametophyte and are recombinant through syngamy. The resulting sporophytes produce dispersing spores, which are recombinant through meiosis. This should better adapt ferns to red-queen selection than strawberry-kin species (*Potentilleae*).

Phylogenetic generalised least squares analyses show that the number of parasitic fungi recorded per species rises significantly with the number of citations per species both for *Potentilleae* and ferns. The slopes also differed significantly from each other and that for strawberry-kin was steeper. Organisms with a strawberry-like life cycle should do better with staying recombinant offspring and dispersing clonal offspring. This would amount to sexually producing runners, tubers, polyps and may well-nigh be impossible. Theoretically, life cycles with recombinant offspring that stay and clonal offspring that disperse should be best adapted against red-queen selection from micro-parasites. The rarity of this 'red-queen life cycle' among multicellular species remains perplexing.

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1. Introduction

1.1 Cost of sexual reproduction

John Maynard Smith provided an analysis of the cost of sexual reproduction as early as 1958. It occurred within his popular science book *The Theory of Evolution*, a contribution to the Pelican Biology Series of paperbacks published by Penguin Books. Here, Maynard Smith clearly attributed the twofold cost of sex to males:

> 'If the rate of increase of an animal population were limited by the number of eggs which each female could lay, which in turn depended on how much food a female could eat and transform into eggs, then a population consisting entirely of parthenogenetic females would increase twice as fast as would a population of equal numbers of males and females. From the point of view of reproduction, males are a waste of living material. (This argument does not hold for hermaphroditic organisms, or for those animals in which both parents help to feed the young.' (Maynard Smith 1958, 138)

When George C. Williams reviewed a paper by Michael T. Ghiselin (1969), he informed Ghiselin about the cost of sex, referring to the second edition of Maynard Smith's Penguin book. Williams already attributed the cost of sex to the genome reduction in meiosis.

> 'Williams, who reviewed the paper for the journal in which it appeared, responded by drawing attention to a point that both of them [Williams and Ghiselin] had overlooked, but that had come to his attention from a book by Maynard Smith (1966): that mictic females pass on half as many genes to the next generation as parthenogenetic females do.' (Ghiselin 1988, 16; see also Williams 1996, xii)

Maynard Smith saw the cost of sex as resources wasted on males (Maynard Smith 1971, 170-2; 1978, 3), Williams as a genetic cost incurred through meiosis (Williams 1971, 13; Williams and Mitton 1973; Williams 1975, 9; 1980, 373; 1988, 294). On the situations under which each concept applies see Lively and Lloyd (1990).

1.2 Maintenance of sexual reproduction

Maynard Smith's point of departure were animal species with diploid body cells, haploid gametes (anisogamous sperm and egg cells), and no brood care by fathers (Maynard Smith 1958, 138; 1971, 170; 1976; 1978, 3). In these species, here referred to as diplontic, a mutation for asexual reproduction will genetically isolate the mutant.

Williams also started from diplontic species but assumed that asexual and sexual reproduction coexisted in the life cycle. That means that the organisms are diploid but they can also reproduce sexually as well as clonally. In this diplontic plus heterogonic life cycle, as it is called (see fig. 1, diplontic with clonal side-cycle), the allocation of resources to the modes of reproduction can gradually shift. Mutations for a bit more asexual reproduction will not isolate the mutant from the population (Williams and Mitton 1973; Williams 1975). According to Williams (1975, 10f), an immediate benefit must balance the cost of sexual reproduction in this stable coexistence with asexual reproduction.

> 'There is no escaping the conclusion that these life cycles must be close to evolutionary equilibrium. The observed incidence of asexual and sexual reproduction must represent for these forms the currently adaptive optimum maintained by selection. In these populations there can be no net disadvantage to sexual reproduction.' (Williams 1975, 11)

Williams (1975) considered a series of diplontic model life cycles that differed in their balance of asexual vs sexual reproduction. The Aphid-Rotifer model comprised species switching between modes of reproduction at certain times. The Strawberry-Coral model switched to sex when the offspring would disperse in space (not time). By the way, Bell (1982) has shown that the life cycles of coelenterates (including corals) are far more diverse than being heterogonic with recombinant propagules that disperse and clonal ones that stay.

> 'In the diversity and mutability of their reproductive habits, the coelenterates have a claim to be the most protean of metazoans.' (Bell 1982, 186)

Anyway, Williams (1975) arrived at diplontic organisms with no asexual reproduction. Here, the evolutionary trade-off seemed to lie at zero investment in asexual reproduction. The Elm-Oyster model comprised such species with a high fecundity. Their average adult females had more than a million offspring per lifetime (zygote-to-zygote-increase: $ZZI > 10^6$). Williams found arguments why high fecundity species should not invest in asexual reproduction (Williams and Mitton 1973; Williams 1975, ch. 4-6). Yet he failed to do so for low fecundity species ($ZZI < 10^3$) such as mammals, birds, and many insects:

> 'Their present exclusive reliance on sexual reproduction must be ascribed to inheritance from a high-fecundity ancestor in which the complete replacement of asexual with sexual reproduction was the evolutionary equilibrium. If and when any form of asexual reproduction becomes feasible in higher vertebrates, it completely replaces sexual. So in these forms sexuality is a maladaptive feature, dating form a piscine of even protochordate ancestor, for which they lack the preadaptation for ridding themselves.' (Williams 1975, 102f)

Maynard Smith (1976, 254) corroborated that the maintenance of sexual reproduction required a high fecundity. Therefore, William D. Hamilton sought an immediate advantage to sex in low-fecundity species.

> ‘Williams himself seems to have despaired of showing advantage for sexuality for low fecundity organisms and concludes, in effect, that most practice sex because they haven’t found suitable tricks for eliminating it yet (can he really believe this for so many vertebrates?).’ (Hamilton 1996 [1975], 365)
>
> ‘My striving to find models that could cope with low fecundity as well as with twofold cost is apparent in all my sex models’ (Hamilton 2001, 17)

1.3 Red-queen selection by micro-parasites

Sexual recombination will only benefit individuals, when the heritability of fitness is negative. This means that genotypes of high fittest in one generation will be of low fitness in the next. Bell (1982, 106) called this selection ‘capricious’ in contrast to merely changeable or unpredictable selection.

Hamilton’s models included capricious selection through pathogens and micro-parasites. Due to their shorter life cycles, they should outpace their hosts in the evolutionary race. These micro-parasites can overcome the defence mechanisms of hosts that clone themselves. They reduce their fitness more than that of hosts reproducing sexually. Hamilton’s models showed that micro-parasites could cause negative heritability of fitness. That is, they could favour sexual reproduction in the short run (Hamilton, Axelrod, and Tanese 1990; Hamilton 2001).

These models have come to be called ‘parasite red queen’ models, after a statement by the Red Queen in Lewis Carroll’s book ‘Through the Looking-Glass’:

> '"A slow sort of country!" said the Queen. "Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!"'

Hamilton's point of departure were organisms with low fecundity (e.g., mammals, birds, and insects like scarabs). Williams' failure to account for exclusively sexual reproduction in low-fecundity species motivated Hamilton. Yet, he never modelled heterogonic life cycles (Williams' point of departure). When expanding from one to many loci, Hamilton switched from diploid to haploid hosts (Hamilton 1980, 286; Hamilton et al. 1990, 3567). [This implies haplontic rather than diplontic life cycles (see fig. 1), with negligible selection in the unicellular stages.] Hamilton took this decision for the ease of modelling (Hamilton 2001, 53), but also for avoiding mere Mendelian allele-swapping as a cause for maintaining sex (Hamilton 2001, 611). A majority of empirical studies supported this Parasite Red Queen hypothesis (e.g., Jokela, Dybdahl, and Lively 2009; Lively and Morran 2014), but some also contradicted it (e.g., Ben-ami and Heller 2005; Tobler and Schlupp 2008).

1.4 A belated challenge of G.C. Williams to the late W.D. Hamilton

Hamilton died unexpectedly in March 2000. Williams could, unfortunately, only pose his last challenge to his friend in a talk at a memorial session for Hamilton (Trivers 2015, 195). The challenge got on record in an obituary made from that talk:

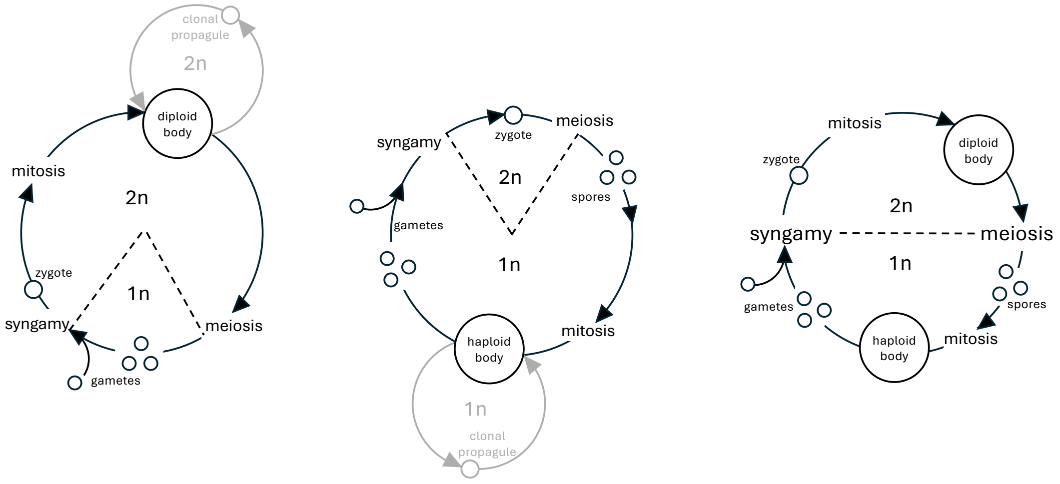
> 'I am not convinced that adaptation by local pathogens to parental genotypes need be the major problem solved by sexuality. I think that the general unpredictability of offspring environments is what provides the main advantage. This issue is most appropriately settled not by modeling or data gathering but by consulting authorities. For a reliable insight on the significance of sexuality there are many appropriate

> authorities, but one that is especially clear is the strawberry plant (Fragaria). Offspring that develop immediately in the parents' environment, with pathogens adapted to those parents' genotypes, will not be sexually produced; whereas those that develop at variable times in the future, over a large range of habitats will be. The allocation of resources to sexual and asexual reproduction must be that which balances the two-fold cost of meiosis by the advantage of genetic diversity among widely dispersed seeds.' (Williams 2000)

The strawberry was Williams' model for a diplontic and heterogonic life cycle with clonal propagules that stay (Dagg 2017, 58f). That means that life cycle differences are crucial for arguments about the cost and maintenance of sex.

1.5 Increasing life-cycle complexity to decrease perplexity

Life cycles that separate the male function from meiosis and should be particularly instructive about the cost and maintenance of sex. Diplontic and haplontic life cycles (heterogonic or not) are not ideal for parsing the cost of meiosis from that of males, because meiosis and male functions are close to each other in development, if not in time. [Mammalian eggs do rest in the prophase of meiosis I for long times, but do not develop during this arrest.] Diplohaplontic life cycles alternate between generations (fig. 1). A diploid multicellular stage produces haploid spores through meiosis, and a haploid multicellular stage produces haploid gametes trough mitosis. Male functions (and syngamy) occurs at a developmental antipode to meiosis.



diplontic haplontic diplohaplontic

Figure 1: Life cycles.

Diplontic: The multicellular stage is diploid and produces haploid gametes that fuse directly to produce diploid zygotes. The heterogonic variant of this life cycle includes a peripheral cycle of diploid bodies producing clonal offspring (shown in grey). Maynard Smith started from the simple diplontic life cycle, where asexual mutants are genetically isolated by default. Williams started from heterogonic life cycles, where mutations that increased or decreased the amount of asexual reproduction were alleles of the same population.

Haplontic: The multicellular stage is haploid and produces gametes that fuse to produce zygotes. They undergo meiosis directly to produce haploid spores. The heterogonic variant of a haplontic life cycle includes a peripheral cycle of haploid bodies producing clonal offspring (shown in grey).

Diplohaplontic: Multicellular diploid and haploid generations occur. The diploid generation (sporophyte) produces recombinant spores through meiosis. These grow into the haploid generation (gametophyte) producing gametes through mitosis. The latter fuse to produce recombinant zygotes through syngamy. Syngamy (fertilisation) and meiosis form developmental antipodes. Heterogonic variants (not shown) could include peripheral cycles as shown in the diplontic and haplontic cycles. The diploid side-cycle does, however, lead into ploidy series in ferns, because the resulting gametophytes produce diploid gametes that fuse etc. [An asexual main cycle exists in ferns, with diploid gametophytes reproducing vegetatively (through gemmae) and diploid sporophytes producing diploid spores through premeiotic endomitosis or first division restitution (see below). That main cycle is not heterogamic however but obligate. That is, it is genetically isolated from the sexual cycle shown.]

Strictly speaking, flowering plants are diplohaplontic (Coelho et al. 2007). The haploid stage is reduced, however, to a few cells in the pollen grain or embryo sac. This reduction of the haploid phase puts meiosis close to syngamy. Therefore, higher plants are lumped with diplontic organisms, despite the existence of a reduced haploid phase (Richerd et al. 1993).

The haploid multicellular stage is called gametophyte, because it produces gametes through mitosis. Gametes are clonal to their parent gametophytes, but the zygotes are recombinant trough syngamy. The diploid, multicellular stage is called the sporophyte, because it produces spores through meiosis. This leads to haploid spores that are recombinant through the independent assortment of non-homologous chromosomes and crossing-over between homologous chromosomes. The cost of sex is spread out over both phases of the life cycle (Richerd et al. 1993) and so is recombination.

A comparison with strawberries requires organisms with this life cycle to be terrestrial, perennial, and herbaceous. Such organisms with almost independent generations of sporophytes and gametophytes are the ferns. Pathogens are rare in ferns (Berkeley 1862; Page 2002, 13). This is surprising since their ecology should promote infections, especially by fungi: dense stands of a single ferns species often occur in shaded and humid areas.

Williams' last challenge to Hamilton (see section 1.4) can give a clue, here. The sporophytes grow on the spot of their parent gametophytes, and they are recombinant. [So are the dispersing haploid spores.] If recombination benefits staying offspring against parental micro-parasites, ferns should be less parasitised than strawberries. Three studies are noteworthy in this respect. The first suggests fern extinction is due to physical (not biological) perturbations (Lehtonen et al. 2017). The other two studies suggest that ferns harbour fewer fungal pathogens than forbs (Helfer 2006; Antonovics 2020). The following tests the hypothesis that ferns are less parasitised than strawberries.

2. Materials and methods

I tested the hypothesis that ferns are parasitised less than strawberries. The number of parasitic fungi recorded for a plant species should increase with the effort of studying that host. The number of citations of a plant species (the binomial species name put into quotation marks) in 'Google Scholar' estimated the effort in studying that species. The records of parasitic fungal species for a plant species come from the Agricultural Research Service (ARS) of the U.S. Department of Agriculture (USDA).

The ARS utilises primary research literature (their sources) to accumulate data on host plants and their fungal diseases into an online searchable database ('USDA Fungal Databases' 2025). A host species that is not mentioned in their sources will not be in their database. Searching the database for such a host species will return: "no results found." However, searching for a host species that is in the fungal database can also return "no results found" at times. Therefore, the reply "no results found" can mean two different things: Either the host species was mentioned in the database's sources, but no fungal parasite was recorded (true negative). Or the host species was not mentioned in its sources, but fungal parasites may be on record in primary literature not (yet) utilized by the USDA Fungal Database (false negative). I excluded host species returning the reply "no results found" from my samples. That is, the samples contain no host species with zero fungal parasites.

An issue with fungal synonyms could arise within the fungal records for one host species. For example, *Marssonia potentillae* could be recorded along with *Marssonia sp.* or *Marssonia potentillae var. tormentillae* for the same host species. These cases were counted as only on record. Hybrids and subspecies were also discounted. When a variety or a 'Genus sp.' entry of a taxon was the only record for a fungal genus (no binomial species name of the same genus on record), it was counted as a datapoint. Multiple records of the same fungus found on the same host but in different countries were counted as only one datapoint.

Testing ferns against strawberries demands a phylogenetic comparative approach, here, phylogenetic generalized least squares (PGLS). This requires phylogenetic trees for the compared taxa. ‘TimeTree of Life’ project synthesizes published studies on molecular sequences and species divergence times (Kumar et al. 2022). Its online knowledge base provides phylogenies for species listed in a text-file, given that the listed species were part of a study synthesized by TimeTree. And it can store the resultant trees in the Newick format.

The species in these phylogenetic trees need to match the species with the fungal records. However, the TimeTree knowledge base cannot place all species from the USDA Fungal Database in a phylogenetic tree. For some species it simply has no data, for others its data do not suffice to properly place them. I excluded these species from my samples. Sometimes the Fungal database used species names known to TimeTree only by a synonym. Some primary sources of the Fungal database are old (e.g., Wiehe 1948). It is no wonder, then, that the taxonomic status of some of the species’ names in the Fungal database has changed. I therefore checked for synonyms, when TimeTree could not identify a species name from the Fungal database. Synonyms were matched using the ‘NCBI Taxonomy Browser’ (Schoch et al. 2020) and the online tool of the Royal Botanic Gardens, Kew (Plants of the World Online 2025).

Because this matching of Fungal with TimeTree records left only 7 strawberry species, the larger taxon *Potentilleae* was chosen. It includes cinquefoils and other genera that all have the strawberry life cycle but drier fruits. This yielded 85 strawberry-kin species. *Polypodiales* were chosen as the appropriate fern taxon (‘Lifemap’ 2025). Excluding species with no USDA fungal record and those that could not be matched with TimeTree left 322 *Polipodiales* species.

PGLS analyses utilized the R package (R Core Team, 2018). The models accorded to:

gls(lgC ~ lgF, data = TaxFun, correlation=corBrownian (1, TaxTree)

Here lgC is the decimal logarithm of the number of citations per species, lgF the decimal logarithm of the number of fungi per species, TaxFun the data-frame for the taxon in question (*Potentilleae* or *Polypodiales* respectively) and TaxTree the covariance matrix derived from the phylogenies in question. A two-sample Welch's t-test (two-tailed) was used to check whether the slopes of the two PGLS analyses were significantly different from each other.

Two plots are purely illustrative. First, the number of citations (lgC) per host species was plotted against the number of fungi (lgF) recorded per host for both samples with their trend lines. These trend lines do not show phylogenetically independent regressions. Second, a logistic model was used to compare the probability of fungal records for host plants. The number of fungi recorded on plant species was transformed into a binary variable. Since "no results found" in the USDA Fungal Database excluded hosts as potential false negatives, hosts with one fungal record received the binary value 0 and hosts with more than one record received the binary value 1. The number of citations (lgC) was the explanatory variable. A linear logistic regression predicted the probability of finding more than one fungus for each species. These predictions were compared with observed probabilities calculated for number of citations grouped into classes of 0-0.5 etc. on a lg-scale. The number of species with more than one record in each class was divided by the sum of species in that class. This ratio was taken as the observed probability for that class. Again, the resulting probability plot does not show phylogenetically independent data-points.

3. Results

For both samples (strawberry-kin and ferns) the PGLS analysis yields a slope that differs significantly from zero (table 1). The Welch's t-test shows that these two slopes also differ significantly from each other (t-statistic = 2.9070, p-value = 0.0059).

Coefficients	Value	Std.Error	t-value	p-value
		Potentileae (strawberry-kin)		
(Intercept)	1.7039	0.5073	3.3589	0.0012
lgF	1.4545	0.0661	22.0125	0.0000
		Polypodiales (ferns)		
(Intercept)	2.3172	1.5913	1.4562	0.1463
lgF	0.8460	0.0697	12.1315	0.0000

Table 1: Generalized least squares fit by REML, Model: lgC ~ lgF, Correlation Structure: corBrownian (with covariance matrix derived from phylogeny of *Potentileae* and *Polypodiales* respectively)

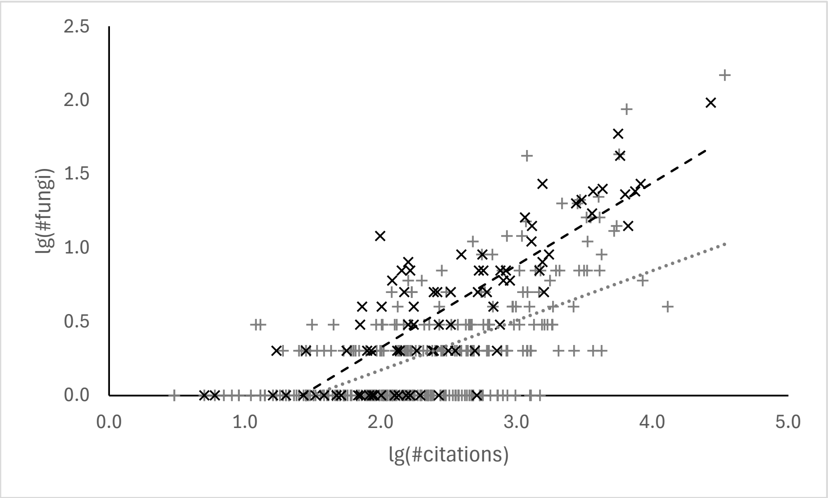


Figure 2: Fungal records in relation to study effort of fern species (grey symbols: +) and strawberry-kin species (black symbols: ×). The trend lines are purely illustrative, as the data-points are not phylogenetically independent.

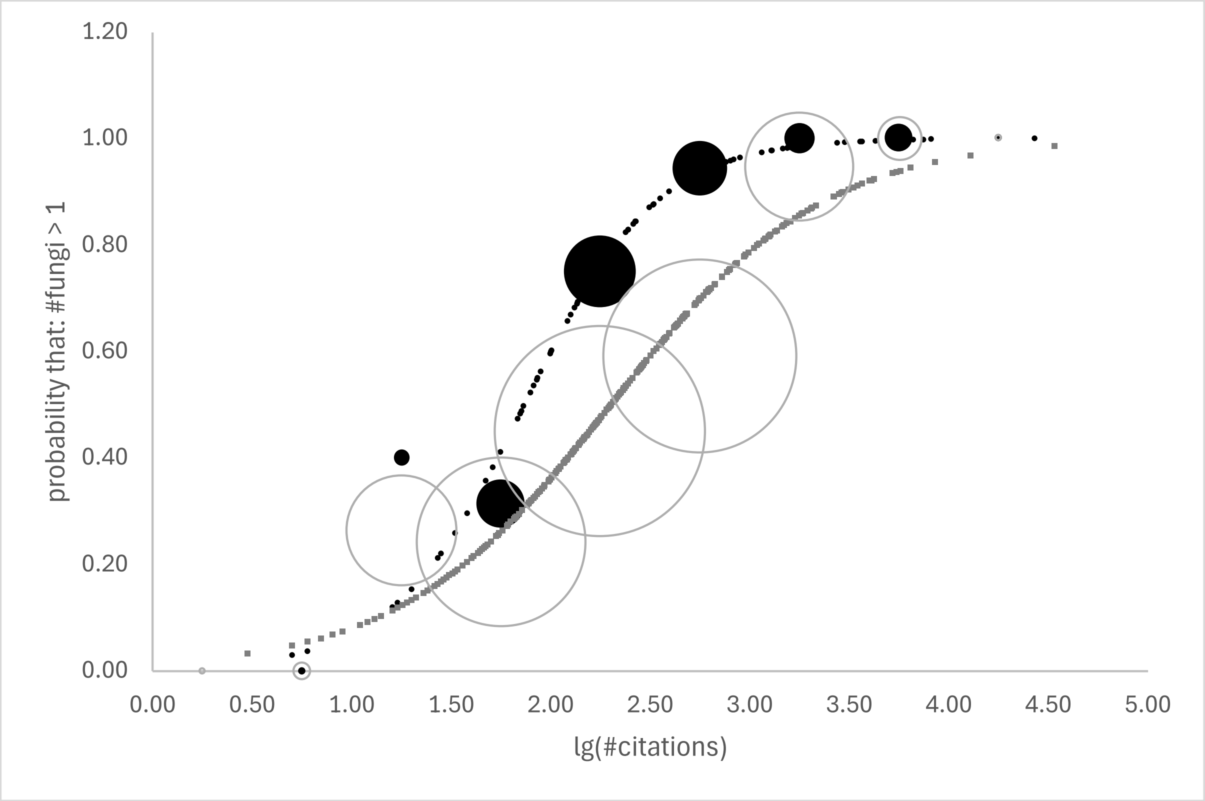


Figure 3: Probability of detecting more than one fungus with respect to the number of citations to the host. The points are predicted from the logistic regression model (see text). The lower series (grey squares) are ferns. Open circles show observed probabilities for ferns and closed circles show observed probabilities for strawberry-kin species. Diameters of the circles are proportional to the number of species in each of the classes.

4. Discussion

4.1 From the paradox of sex to Fern Land

Section 1 revisited the pioneers of what has become known as the evolutionary paradox of sexual reproduction. Their theoretical arguments lead to W. D. Hamilton's parasite red-queen model and George C. Williams' last challenge to it. Unfortunately, Hamilton had died unexpectedly, and Williams could only present it in a memorial talk (Trivers 2015, 195) and an obituary notice made from it (Williams 2000). This challenge has hitherto been ignored, except for a history-of-science article (Dagg 2017, 58). Williams raised the widespread diplontic and heterogonic life cycle (fig. 1) of organisms like strawberries as a contradiction to expectations from red-queen theory. They propagate contrary to what would be adaptive under red-queen selection. Their recombinant offspring disperses, and their clonal offspring stays close to the parent. This means that life cycle differences are important for the cost and maintenance of sexual reproduction. A life cycle spreading recombination over all its stages seemed preferable over the strawberry life cycle. Hence, the diplohaplontic life cycle became the point of departure into a quantitative analysis, and ferns became the best candidates for comparison with strawberry-like plants as both are terrestrial, perennial, and herbaceous.

4.2 Testing strawberries against ferns

The haploid spores of ferns are recombinant through meiosis and disperse before growing into haploid gametophytes. They produce haploid gametes that fuse to produce diploid zygotes. These are recombinant through syngamy. That is, recombination is spread out over the whole life cycle. The zygote grows into a sporophyte, in situ, on the maternal gametophyte. Staying offspring that is recombinant should do better under red-queen selection than the clonal offspring of strawberries. That ferns indeed have few microbial parasites turned out to be an aged lore among botanists (Berkeley 1862; Page 2002, 13) with some quantitative support from Helfer (2006) and Antonovics (2020).

We tested the relationship between the number of parasitic fungi recorded per species and the number of citations per species in strawberry-kin species (*Potentilleae*) and *Polypodiales* ferns respectively (see table 1). Fern species should have fewer fungi, because their life cycle is better adapted to red-queen selection by micro-parasites. Phylogenetic Generalised Least Squares analyses showed for both taxa that the slopes differed significantly from zero. A Welch's two-sample t-test showed that the slopes also differed significantly from each other (see results). And that for the strawberry-kin was steeper than that for the ferns. This suggests that heterogonic life cycles with clonal staying offspring are not optimal vis-à-vis micro-parasites.

4.3 Conclusion

If a heterogonic organisms (diplontic or haplontic) under red-queen selection could choose, its staying offspring should be recombinant and its dispersing offspring clonal. Let us call this the 'red-queen life cycle'. Alas, the 'strawberry life cycle' has the opposite combinations of modes of dispersal and reproduction. The 'fern life cycle' is a third kind, as it is diplohaplontic, not heterogonic, and recombination is spread over all its stages.

Ferns show that a life cycle exists that is better adapted to micro-parasites than the strawberry life cycle. Having a better heterogonic life cycle, a red-queen life cycle, would amount to sexually producing rhizomes, stolons, tubers etc. for most plants. This may well-nigh be an evolutionary impossibility. Organisms with a strawberry life cycle do not produce staying offspring asexually because that is optimal vis-à-vis microbial parasites, but because their life cycle did not offer a way to produce them sexually. The strawberry life cycle constrains organisms from an optimal adaptation against micro-parasites.

A surprising question remains: Why do red-queen life cycles (with dispersing clonal propagules and staying recombinant ones) not dominate multicellular life? Micro-parasites were a selective force throughout the evolution of multicellularity. If dispersal meant escape from parental parasites, saving the cost of sex on dispersing propagules but incurring it for staying ones should be the optimal strategy against micro-parasites. A red-queen life cycle should be even better than a diplohaplontic one, spreading recombination (meiosis and syngamy) over the whole cycle. Yet, most multicellular species have different life cycles.

A systematic search for organisms with red-queen life cycles hardly retrieved any. A rare one exists in haplontic *Peritricha* (Ciliophora) of the genus *Zoothamnium*. Sexual reproduction has not been observed in the largest and best studied species of the genus, *Z. niveum* (Fauré-Frémiet 1930, 47; Rinke et al. 2007; Bright et al. 2014), whose colonies live for seven days on average and up to 11 days (Ott et al. 2004; Rinke et al. 2007). Sexual reproduction does occur, however, in *Z. alternans* and *Z. arbuscula* (Furssenko 1929; Summers 1938, 126; Herron et al. 2013, 11). A haploid colony produces haploid (clonal) swarmers and microgamonts that both disperse. The swarmer grows into a new haploid colony elsewhere, the microgamont fuses with a macrogamont of another colony. The resulting diploid part is recombinant through syngamy. It undergoes meiosis producing haploid parts of the colony that are recombinant through syngamy & meiosis. These recombinant parts all stay in the colony. That is, the recombinant offspring stays in situ, while the clonal offspring grows expatriate. Most colonies produce only two macrogamonts that can fuse with microgamonts (Furssenko 1929; Summers 1938). This and the short lifespan of colonies limit the extent to which they can become genetic mosaics.

Anyway, red-queen life cycles hardly form a considerable part of multicellular life. This wants an explanation!

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Appendix

1. Fern species

1.1 *Polypodiales* data

CSV format: species, number of citations, number of fungi recorded; semicolons replace line breaks. * mark species names recognized by TimeTree, for which the USDA Fungal Database used synonyms. These synonyms are given in the note at the end of the list.

Acrostichum_aureum,4200,2; Adiantum_aleuticum,318,1; Adiantum_capillus-veneris,8480,6; Adiantum_cristatum,28,2; Adiantum_jordanii,199,1; Adiantum_latifolium,476,11; Adiantum_pedatum,3320,11; Adiantum_petiolatum,105,2; *Adiantum_philippense,1595,3; *Adiantum_raddianum,851,1; Adiantum_reniforme,287,1; Adiantum_silvaticum,14,1; Adiantum_subcordatum,14,1; Adiantum_tetraphyllum,159,6; Adiantum_venustum,615,3; Aleuritopteris_farinosa,126,1; Aleuritopteris_kuhnii,13,1; *Amauropelta_atrovirens,16,1; *Amauropelta_oligocarpa,54,1; *Amauropelta_rudis,78,2; *Amblovenatum_opulentum,90,1; *Anchistea_virginica,1338,3; *Anisocampium_niponicum,562,1; *Arachniodes_amabilis,65,2; *Arachniodes_aristata,290,2; *Arachniodes_miqueliana,41,1; *Arachniodes_simplicior,48,1; *Arachniodes_standishii,174,1; Arthropteris_beckleri,36,1; *Ascogrammitis_anfractuosa,13,1; Asplenium_adiantum-nigrum,1480,1; Asplenium_aethiopicum,470,1; Asplenium_antiquum,173,1; Asplenium_bulbiferum,786,7; Asplenium_cristatum,134,2; *Asplenium_dareoides,90,1; Asplenium_flaccidum,435,2; Asplenium_incisum,375,1; Asplenium_monanthes,475,1; Asplenium_nidus,3270,16; Asplenium_oblongifolium,278,2; Asplenium_onopteris,462,1; Asplenium_polyodon,371,1; Asplenium_radicans,80,1; Asplenium_ruta-muraria,1820,3; Asplenium_rutifolium,79,1; Asplenium_scolopendrium,1270,1; Asplenium_septentrionale,938,4; Asplenium_trichomanes,3660,2; *Athyrium_asplenioides,456,3; Athyrium_clivicola,19,1; *Athyrium_distentifolium,1169,15; *Athyrium_filix-femina,6426,87; Athyrium_iseanum,69,2; Athyrium_melanolepis,26,2; Athyrium_otophorum,69,1; Athyrium_spinulosum,50,1; *Athyrium_subrigescens,9,1; Athyrium_vidalii,105,1; Athyrium_yokoscense,857,2;

*Austroblechnum_fernandezianum,129,2; Blechnopsis_orientalis,1458,5; Blechnum_occidentale,662,9; Blechnum_polypodioides,147,1; Blechnum_punctulatum,61,1; Blotiella_pubescens,17,1; *Bosmania_membranacea,130,2; *Calciphilopteris_ludens,97,1; *Campyloneurum_phyllitidis,304,5; Ceratopteris_thalictroides,2030,2; Cheilanthes_chusana,32,1; *Cheilanthes_mollis,221,1; *Cheilanthes_nitidula,48,1; Cheilanthes_viridis,445,3; *Christella_acuminata,209,3; *Christella_dentata,1258,2; *Christella_hispidula,224,1; Christella_parasitica,469,2; Coniogramme_fraxinea,141,2; Coniogramme_intermedia,169,5; Coniogramme_japonica,168,5; Coniogramme_suprapilosa,3,1; Cryptogramma_acrostichoides,361,2; Cryptogramma_brunoniana,53,1; Cryptogramma_crispa,791,1; Cryptogramma_stelleri,458,2; *Ctenitis_subglandulosa,53,2; Cyclopeltis_semicordata,126,3; Cyrtomium_falcatum,1090,12; Cyrtomium_fortunei,567,3; Cystopteris_alpina,117,1; Cystopteris_bulbifera,982,4; Cystopteris_fragilis,4060,16; *Cystopteris_moupinensis,45,3; Cystopteris_sudetica,82,1; *Davallia_solida,621,2; Davallia_trichomanoides,200,6; *Dennstaedtia_cicutaria,147,3; Dennstaedtia_hirsuta,197,1; *Dennstaedtia_obtusifolia,67,1; Dennstaedtia_punctilobula,1830,3; Dennstaedtia_scabra,144,1; *Deparia_acrostichoides,667,4; *Deparia_confluens,25,1; Deparia_japonica,170,1; Deparia_longipes,6,1; Deparia_orientalis,21,1; *Deparia_pterorachis,60,2; Deparia_pycnosora,152,2; Deparia_tenuifolia,9,1; *Diplazium_bantamense,122,1; Diplazium_esculentum,2640,2; Diplazium_hians,28,1; Diplazium_kawakamii,29,1; Diplazium_lindbergii,25,1; Diplazium_maximum,164,2; Diplazium_mettenianum,57,1; Diplazium_squamigerum,63,2; Diplazium_wichurae,66,1; Doodia_media,213,1; Doryopteris_pedata,120,5; *Dryopteris_affinis,1050,3; Dryopteris_amurensis,38,2; *Dryopteris_apiciflora,44,1; Dryopteris_arguta,368,3; Dryopteris_austriaca,584,5; Dryopteris_azorica,46,1; Dryopteris_bissetiana,226,3; Dryopteris_borreri,303,2; *Dryopteris_carthusiana,4010,22; *Dryopteris_championii,116,1; Dryopteris_chinensis,294,1; Dryopteris_clarkei,12,3; Dryopteris_crassirhizoma,1950,7; Dryopteris_cristata,1250,1; Dryopteris_dilatata,2150,20; Dryopteris_erythrosora,839,2; Dryopteris_filix-mas,5690,43; Dryopteris_gymnophylla,40,1; Dryopteris_inaequalis,109,1; Dryopteris_intermedia,1110,2; Dryopteris_lacera,251,2; Dryopteris_marginalis,1240,4; *Dryopteris_maximowicziana,21,1;

Dryopteris_monticola,119,1; *Dryopteris_pallida,162,1; Dryopteris_sabae,3,1; Dryopteris_sacrosancta,110,1; Dryopteris_saxifraga,107,1; Dryopteris_sparsa,223,1; *Dryopteris_varia,270,3; Elaphoglossum_cuspidatum,23,1; *Elaphoglossum_gayanum,47,1; Elaphoglossum_latifolium,97,1; *Goniophlebium_amoenum,99,2; Goniophlebium_percussum,54,1; *Goniopteris_abrupta,28,1; *Goniopteris_poiteana,61,2; *Goniopteris_tetragona,93,2; *Grammitis_pseudaustralis,20,1; *Gymnocarpium_disjunctum,205,2; *Gymnocarpium_dryopteris,2883,7; Gymnocarpium_jessoense,85,1; Gymnocarpium_robertianum,480,2; *Haplopteris_flexuosa,156,1; Hemionitis_arifolia,395,1; Histiopteris_incisa,1200,2; *Hymenasplenium_unilaterale,357,1; Hypolepis_punctata,350,2; Hypolepis_repens,159,2; Hypolepis_sparsisora,76,1; *Icarus_filiformis,238,2; Lastreopsis_hispida,122,1; *Lepidomicrosorium_buergerianum,29,1; *Lepidomicrosorium_superficiale,30,1; Leptogramma_mollissima,28,1; Leptogramma_totta,30,2; Lindsaea_lancea,166,3; Lindsaea_trichomanoides,109,1; Lindsaea_ulei,13,3; *Lomaria_discolor,551,5; *Lomariocycas_schomburgkii,21,1; Lomariopsis_japurensis,83,1; *Lomariopsis_vestita,53,1; *Lorinseria_areolata,1186,2; Macrothelypteris_torresiana,606,2; *Matteuccia_struthiopteris,2932,21; *Meniscium_serratum,127,1; Metathelypteris_laxa,19,2; *Microgramma_lycopodioides,230,1; *Microgramma_megalophylla,34,2; Microgramma_squamulosa,191,2; Microlepia_marginata,151,1; Microlepia_speluncae,477,1; Microlepia_strigosa,416,1; Microlepia_trichocarpa,18,1; *Microsorum_punctatum,555,9; *Myriopteris_myriophylla,72,1; *Myriopteris_pringlei,60,1; Nephrolepis_auriculata,426,2; Nephrolepis_biserrata,1760,6; Nephrolepis_cordifolia,1850,4; Nephrolepis_exaltata,2800,20; Nephrolepis_falcata,186,1; Nephrolepis_hirsutula,483,2; Nephrolepis_obliterata,77,1; Nephrolepis_pendula,92,3; Nephrolepis_rivularis,101,3; *Niphidium_crassifolium,330,3; *Notogrammitis_angustifolia,92,1; *Notogrammitis_billardierei,139,2; *Oceaniopteris_gibba,103,1; *Odontosoria_chinensis,466,3; Oleandra_articulata,122,1; Onoclea_sensibilis,5220,13; Onychium_japonicum,380,2; *Osmolindsaea_japonica,14,1; *Parablechnum_capense,339,1; *Parablechnum_minus,27,1; *Parablechnum_procerum,251,2; *Pelazoneuron_abruptum,33,1; *Pelazoneuron_patens,101,2; Pellaea_andromedifolia,257,2; Pellaea_glabella,536,1;

Pellaea_mucronata,216,1; Pellaea_pteroides,28,1; Pellaea_rotundifolia,281,7; Pellaea_ternifolia,300,1; *Pentagramma_triangularis,301,1; Phegopteris_connectilis,1110,5; Phegopteris_decursive-pinnata,138,2; *Physematium_oreganum,372,1; *Pityrogramma_calomelanos,2064,7; Pityrogramma_sulphurea,25,2; Pityrogramma_trifoliata,146,1; Platycerium_alcicorne,156,2; Platycerium_bifurcatum,847,12; Platycerium_grande,178,1; Platycerium_wallichii,98,1; Pleopeltis_astrolepis,105,1; *Pleopeltis_polypodioides,1529,3; Polybotrya_osmundacea,88,1; Polypodium_californicum,270,4; Polypodium_cambricum,428,1; *Polypodium_glycyrrhiza,627,3; Polypodium_hesperium,234,1; Polypodium_interjectum,284,2; Polypodium_plesiosorum,93,1; Polypodium_virginianum,1200,5; Polypodium_vulgare,5440,14; Polystichum_acrostichoides,2620,4; Polystichum_aculeatum,1370,7; Polystichum_braunii,770,2; Polystichum_craspedosorum,101,1; Polystichum_hancockii,24,1; Polystichum_igaense,5,1; Polystichum_lepidocaulon,67,1; Polystichum_lonchitis,1050,7; *Polystichum_luctuosum,131,1; Polystichum_munitum,3480,16; *Polystichum_polyblepharum,169,2; Polystichum_pseudomakinoi,8,1; Polystichum_pungens,50,1; Polystichum_setiferum,932,4; Polystichum_squarrosum,211,1; Polystichum_tripteron,421,3; Polystichum_vestitum,554,1; Polytaenium_feei,43,2; Pseudophegopteris_aurita,38,1; Pteridium_aquilinum,33900,148; Pteridium_caudatum,392,2; *Pteridium_esculentum,4212,9; Pteridium_revolutum,273,1; Pteris_biaurita,624,3; Pteris_cretica,3280,7; Pteris_deflexa,103,3; Pteris_dispar,112,1; Pteris_ensiformis,1490,7; Pteris_excelsa,138,1; Pteris_fauriei,221,1; Pteris_longifolia,638,1; Pteris_multifida,1270,2; Pteris_natiensis,7,1; Pteris_orizabae,53,1; Pteris_podophylla,87,1; Pteris_quadriaurita,527,2; Pteris_semipinnata,481,1; Pteris_tremula,727,1; Pteris_vittata,12900,4; Pteris_wallichiana,239,1; Pyrrosia_adnascens,195,1; Pyrrosia_lingua,723,1; Pyrrosia_petiolosa,244,1; Pyrrosia_serpens,164,1; *Rhachidosorus_mesosorus,55,1; *Rumohra_adiantiformis,1192,42; *Saccoloma_domingense,28,1; Sadleria_cyatheoides,277,1; *Salpichlaena_volubilis,180,2; *Selliguea_malacodon,11,1; *Serpocaulon_adnatum,20,1; *Serpocaulon_triseriale,133,4; Stenochlaena_palustris,1690,3; Stenochlaena_tenuifolia,131,3; *Struthiopteris_amabilis,28,2; *Struthiopteris_spicant,3135,7; Tectaria_harlandii,17,1; Tectaria_heracleifolia,220,2; Tectaria_martinicensis,31,3; *Telmatoblechnum_indicum,279,2; *Telmatoblechnum_serrulatum,957,3; *Thelypteris_palustris,4085,7;

Triplophyllum_dicksonioides,32,1; Woodsia_glabella,431,2; Woodsia_obtusa,981,1; Woodsia_polystichoides,233,1; Woodsia_scopulina,447,1; Woodwardia_fimbriata,286,2; Woodwardia_japonica,533,1; Woodwardia_orientalis,148,2; Woodwardia_radicans,604,2; *Zealandia_pustulata,353,1

*Note:

For the asterisk-marked species the USDA Fungal Database used the following synonyms: *Adiantum philippense syn. Adiantum lunulatum; *Adiantum raddianum syn. Adiantum decorum; *Amauropelta oligocarpa syn. Thelypteris oligocarpa; *Amauropelta rudis syn. Thelypteris rudis; *Amblovenatum opulentum syn. Thelypteris opulenta; *Anchistea virginica syn. Woodwardia virginica; *Anisocampium niponicum syn. Athyrium niponicum; *Arachniodes amabilis syn. Polystichum amabile; *Arachniodes aristata syn. Polystichum aristatum; *Arachniodes miqueliana syn. Dryopteris miqueliana; *Arachniodes simplicior syn. Rumohra simplicior; *Arachniodes standishii syn. Rumohra standishii; *Ascogrammitis anfractuosa syn. Polypodium induens; *Asplenium dareoides syn. Asplenium magellanicum; *Athyrium asplenioides syn. Athyrium angustum; *Athyrium distentifolium syn. Athyrium alpestre; *Athyrium filix-femina syn. Asplenium filix-femina; *Athyrium subrigescens syn. Athyrium elegans; *Austroblechnum fernandezianum syn. Blechnum blechnoides; *Bosmania membranacea syn. Microsorum membranaceum; *Calciphilopteris ludens syn. Doryopteris ludens; *Campyloneurum phyllitidis syn. Polypodium phyllitidis; *Cheilanthes mollis syn. Notholaena sinuata; *Cheilanthes nitidula syn. Mildella nitidula; *Christella acuminata syn. Cyclosorus acuminatus; *Christella dentata syn. Cyclosorus dentatus; *Christella hispidula syn. Thelypteris hispidula; *Ctenitis subglandulosa syn. Ctenitis subtripinnata; *Cystopteris moupinensis syn. Cystopteris sphaerocarpa; *Davallia solida syn. Davallia fejeensis; *Dennstaedtia cicutaria syn. Dennstaedtia rubiginosa; *Dennstaedtia obtusifolia syn. Dennstaedtia ordinata; *Deparia acrostichoides syn. Athyrium acrostichoides; *Deparia confluens syn. Diplazium grammitoides; *Deparia pterorachis syn. Athyrium pterorachis; *Diplazium bantamense syn. Asplenium alternifolium; *Dryopteris affinis syn. Dryopteris paleacea; *Dryopteris apiciflora syn. Ctenitis apiciflora; *Dryopteris carthusiana syn. Dryopteris spinulosa; *Dryopteris championii syn. Dryopteris championi; *Dryopteris maximowicziana syn. Ctenitis maximowicziana; *Dryopteris pallida syn. Dryopteris raddeana; *Dryopteris varia syn. Dryopteris yabei; *Elaphoglossum gayanum syn.

Elaphoglossum leptophyllum; *Goniophlebium amoenum syn. Polypodium amoenum; *Goniopteris abrupta syn. Thelypteris abrupta; *Goniopteris poiteana syn. Thelypteris poiteana; *Goniopteris tetragona syn. Thelypteris tetragona; *Grammitis pseudaustralis syn. Polypodium nanum; *Gymnocarpium disjunctum syn. Dryopteris disjuncta; *Gymnocarpium dryopteris syn. Phegopteris dryopteris; *Haplopteris flexuosa syn. Vittaria flexuosa; *Hymenasplenium unilaterale syn. Asplenium unilaterale; *Icarus filiformis syn. Blechnum filiforme; *Lepidomicrosorium buergerianum syn. Microsorum buergerianum; *Lepidomicrosorium superficiale syn. Polypodium superficiale; *Lomaria discolor syn. Blechnum discolor; *Lomariocycas schomburgkii syn. Lomaria imperialis; *Lomariopsis vestita syn. Stenochlaena vestita; *Lorinseria areolata syn. Woodwardia areolata; *Matteuccia struthiopteris syn. Onoclea struthiopteris; *Meniscium serratum syn. Thelypteris serrata; *Microgramma lycopodioides syn. Polypodium lycopodioides; *Microgramma megalophylla syn. Polypodium schomburgkianum; *Microsorum punctatum syn. Polypodium punctatum; *Myriopteris myriophylla syn. Cheilanthes elegans; *Myriopteris pringlei syn. Cheilanthes pringlei; *Niphidium crassifolium syn. Polypodium crassifolium; *Notogrammitis angustifolia syn. Grammitis magellanica; *Notogrammitis billardierei syn. Grammitis billardierei; *Oceaniopteris gibba syn. Blechnum gibbum; *Odontosoria chinensis syn. Davallia tenuifolia; *Osmolindsaea japonica syn. Lindsaea japonica; *Parablechnum capense syn. Blechnum capense; *Parablechnum minus syn. Blechnum minor; *Parablechnum procerum syn. Blechnum procerum; *Pelazoneuron abruptum syn. Thelypteris grandis; *Pelazoneuron patens syn. Thelypteris patens; *Pentagramma triangularis syn. Pityrogramma triangularis; *Physematium oreganum syn. Woodsia oregana; *Pityrogramma calomelanos syn. Pityrogramma calomelaena; *Pleopeltis polypodioides syn. Polypodium polypodioides; *Polypodium glycyrrhiza syn. Polypodium occidentale; *Polystichum luctuosum syn. Polystichum tsus-simense; *Polystichum polyblepharum syn. Polystichum japonicum; *Pteridium esculentum syn. Pteridium arachnoideum; *Rhachidosorus mesosorus syn. Athyrium mesosorum; *Rumohra adiantiformis syn. Polystichum adiantiforme; *Saccoloma domingense syn. Orthiopteris domingensis; *Salpichlaena volubilis syn. Blechnum volubile; *Selliguea malacodon syn. Polypodium malacodon; *Serpocaulon adnatum syn. Polypodium adnatum; *Serpocaulon triseriale syn. Polypodium brasiliense; *Struthiopteris amabilis syn. Spicantopsis amabilis; *Struthiopteris spicant syn. Blechnum spicant; *Telmatoblechnum indicum syn. Blechnum indicum; *Telmatoblechnum serrulatum syn. Blechnum serrulatum; *Thelypteris palustris syn. Thelypteris thelypteris; *Zealandia pustulata syn. Microsorum pustulatum

1.2 *Polypodiales* tree

Newick format:

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2. Strawberry-kin species

2.1 *Potentilleae* data

CSV format: species, number of citations, number of fungi recorded; semicolons replace line breaks. * mark species names recognized by TimeTree, for which the USDA Fungal Database used synonyms. These synonyms are given in the footnote at the end of the list.

*Alchemilla_acutiloba,159,8; *Alchemilla_alpina,1278,11; *Alchemilla_arvensis,1587,5; Alchemilla_conjuncta,70,3; *Alchemilla_cryptantha,47,1; *Alchemilla_flabellata,121,6; *Alchemilla_glabra,392,9; Alchemilla_glaucescens,175,4; *Alchemilla_gracilipes,73,4; Alchemilla_japonica,27,1; *Alchemilla_microcarpa,313,2; *Alchemilla_mollis,893,6; Alchemilla_saxatilis,33,1; Alchemilla_schizophylla,6,1; *Alchemilla_vulcanica,79,2; Alchemilla_vulgaris,3588,17; *Alchemilla_xanthochlora,569,7; Chamaerhodos_erecta,266,1; *Comarum_palustre,5750,42; Comarum_salesovianum,86,1; Dasiphora_davurica,16,1; *Dasiphora_fruticosa,6630,14; *Drymocallis_arguta,165,7; *Drymocallis_glandulosa,99,12; Fragaria_chiloensis,5590,59; Fragaria_moschata,675,4; Fragaria_nilgerrensis,510,1; Fragaria_nipponica,165,1; Fragaria_orientalis,605,5; Fragaria_virginiana,8141,27; Fragaria_vesca,26900,96; Horkelia_tridentata,38,1; Potentilla_alba,753,3; *Potentilla_ancistrifolia,244,2; Potentilla_anglica,245,5; Potentilla_anserina,7420,24; Potentilla_argentea,2740,20; *Potentilla_atrosanguinea,712,2; Potentilla_aurea,756,7; Potentilla_biennis,82,1; Potentilla_biflora,137,2; Potentilla_caulescens,159,3; *Potentilla_cinerea,797,6; Potentilla_concinna,184,2; Potentilla_crantzii,829,7; Potentilla_curviseta,20,1; Potentilla_diversifolia,519,5; *Potentilla_douglasii,89,1; *Potentilla_effusa,174,3; Potentilla_erecta,6280,23; Potentilla_eriocarpa,68,1; Potentilla_flabellifolia,142,7; Potentilla_freyniana,524,7; *Potentilla_gordonii,148,5; Potentilla_gracilis,1290,14; Potentilla_grandiflora,101,4; *Potentilla_hirta,259,5; Potentilla_hookeriana,100,1; *Potentilla_indica,3648,24; *Potentilla_neumaniana,238,2; Potentilla_newberryi,28,2; *Potentilla_niponica,5,1; Potentilla_norvegica,1540,27; Potentilla_pensylvanica,326,3; Potentilla_pulcherrima,267,3; Potentilla_recta,3000,21;

Potentilla_reptans,4270,25; Potentilla_rivalis,132,2; Potentilla_saundersiana,353,2; *Potentilla_sericoleuca,17,2; Potentilla_simplex,1540,8; Potentilla_speciosa,135,1; Potentilla_sterilis,560,9; Potentilla_stipularis,56,2; Potentilla_stolonifera,51,1; *Potentilla_supina,1149,16; Potentilla_tanacetifolia,493,2; Potentilla_thuringiaca,328,5; Potentilla_uniflora,126,1; Potentilla_vahliana,71,1; Sibbaldia_cuneata,194,1; Sibbaldia_parviflora,154,1; Sibbaldia_procumbens,1730,9; Sibbaldianthe_adpressa,85,2; *Sibbaldianthe_bifurca,1464,7

*Note:

For the asterisk-marked species the USDA Fungal Database used the following synonyms: *Alchemilla acutiloba syn. Alchemilla indivisa; *Alchemilla alpina syn. Alchemilla alpigena; *Alchemilla arvensis syn. Aphanes arvensis; *Alchemilla cryptantha syn. Alchemilla madagascariensis; *Alchemilla flabellata syn. Alchemilla pubescens; *Alchemilla glabra syn. Alchemilla alpestris; *Alchemilla gracilipes syn. Alchemilla pedata; *Alchemilla microcarpa syn. Aphanes microcarpa; *Alchemilla mollis syn. Alchemilla montana; *Alchemilla vulcanica syn. Alchemilla sericata; *Alchemilla xanthochlora syn. Alchemilla pratensis; *Comarum palustre syn. Potentilla palustris; *Dasiphora fruticosa syn. Potentilla fruticosa; *Drymocallis arguta syn. Potentilla arguta; *Drymocallis glandulosa syn. Potentilla glandulosa; *Potentilla ancistrifolia syn. Potentilla dickinsii; *Potentilla atrosanguinea syn. Potentilla argyrophylla; *Potentilla cinerea syn. Potentilla arenaria; *Potentilla douglasii syn. Horkelia fusca; *Potentilla effusa syn. Potentilla collina; *Potentilla gordonii syn.s Horkelia gordonii, Ivesia gordonii; *Potentilla hirta syn. Potentilla astracanica; *Potentilla indica syn. Duchesnea indica; *Potentilla neumaniana syn. Potentilla neumanniana; *Potentilla niponica syn. Potentilla nipponica; *Potentilla sericoleuca syn. Ivesia sericoleuca; *Potentilla supina syn. Potentilla paradoxa; *Sibbaldianthe bifurca syn. Potentilla bifurca

2.2 *Potentilleae* tree

Newick format:

((((Sibbaldia_parviflora:5.43894000,Sibbaldia_procumbens:5.43894000)'14':2.19106000,Sibbaldia_cuneata:7.63000000)'13':18.30000000,(*Sibbaldianthe_bifurca:7.50000000,Sibbaldianthe_adpressa:7.50

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000000)'25':18.43000000)'37':7.13522000,(((((((((*Dasiphora_fruticosa:3.10000000,Dasiphora_davurica:3.10000000)'36':6.43832000,(*Drymocallis_glandulosa:0.92000000,*Drymocallis_arguta:0.92000000)'35':8.61832000)'34':0.00000000,Chamaerhodos_erecta:9.53832000)'43':12.35516000,(((((((((*Alchemilla_xanthochlora:0.37000000,*Alchemilla_acutiloba:0.37000000)'33':1.44000000,Alchemilla_japonica:1.81000000)'51':0.63000000,(Alchemilla_vulgaris:1.62500000,*Alchemilla_glabra:1.62500000)'50':0.81500000)'49':0.96000000,(*Alchemilla_mollis:1.66000000,*Alchemilla_flabellata:1.66000000)'57':1.74000000)'60':0.87000000,Alchemilla_conjuncta:4.27000000)'56':5.24203000,(Alchemilla_saxatilis:2.12000000,*Alchemilla_alpina:2.12000000)'48':7.39203000)'63':0.00000000,(*Alchemilla_arvensis:0.49000000,*Alchemilla_microcarpa:0.49000000)'47':9.02203000)'68':12.13129000,((*Alchemilla_gracilipes:3.65000000,(*Alchemilla_cryptantha:1.66000000,Alchemilla_schizophylla:1.66000000)'73':1.99000000)'72':13.31000000,*Alchemilla_vulcanica:16.96000000)'84':4.68332000)'87':0.00000000,(Fragaria_orientalis:17.05587000,((((Fragaria_nilgerrensis:3.88346000,(Fragaria_virginiana:0.21966000,Fragaria_chiloensis:0.21966000)'83':3.66380000)'82':2.98108000,Fragaria_nipponica:6.86454000)'80':0.14716000,Fragaria_vesca:7.01170000)'79':2.36830000,Fragaria_moschata:9.38000000)'94':7.67587000)'92':4.58745000)'78':0.25016000)'98':0.50032000,(Alchemilla_glaucescens:20.99177000,(*Comarum_palustre:15.99000000,Comarum_salesovianum:15.99000000)'97':5.00177000)'77':1.40203000)'71':0.94962000,((((((((*Potentilla_sericoleuca:8.17211000,((Horkelia_tridentata:3.02574000,*Potentilla_douglasii:3.02574000)'67':1.70033000,*Potentilla_gordonii:4.72607000)'66':3.44604000)'46':5.35633000,Potentilla_biennis:13.52844000)'32':1.15254000,*Potentilla_ancistrifolia:14.68098000)'106':3.77813000,(((((((((Potentilla_saundersiana:2.91086000,*Potentilla_supina:2.91086000)'104':0.00000000,Potentilla_flabellifolia:2.91086000)'103':0.21200000,Potentilla_concinna:3.12286000)'31':1.16934000,Potentilla_norvegica:4.29220000)'30':0.69713000,((((((Potentilla_hookeriana:0.79508000,Potentilla_rivalis:0.79508000)'111':0.21085000,Potentilla_pensylvanica:1.00593000)'29':0.92880000,Potentilla_tanacetifolia:1.93473000)'28':0.84311000,Potentilla_vahliana:2.77784000)'24':0.31867000,((Potentilla_argentea:1.89216000,Potentilla_recta:1.89216000)'116':0.83935000,*Potentilla_niponica:2.73151000)'124':0.36500000)'123':1.23541000,(Potentilla_diversifolia:2.47512000,Potentilla_gracilis:2.47512000)'128':1.85680000)'122':0.65741000)'121':1.79941000,*Potentilla_atrosanguinea:6.78874000)'120':0.00000000,((*Potentilla_neumaniana:4.98215000,*Potentilla_cinerea:4.98215000)'136':0.7
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8999000,*Potentilla_hirta:5.77214000)'134':1.01660000)'139':4.07289000,(((Potentilla_grandiflora:7.
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mplex:3.21812000)'21':1.63774000,Potentilla_reptans:4.85586000)'157':7.94414000,(Potentilla_aurea
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37305000)'163':5.84209000)'161':2.11544000,(((Potentilla_curviseta:9.92805000,Potentilla_eriocarpa:
9.92805000)'153':4.25816000,Potentilla_biflora:14.18621000)'170':1.60122000,(Potentilla_speciosa:1
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