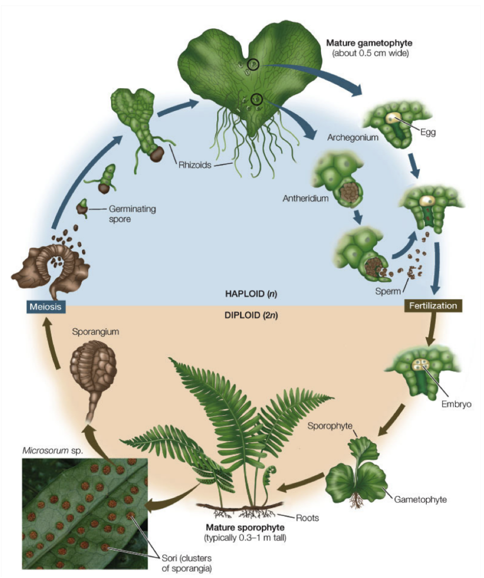
Origins of Anisogamy

(Adaptive Dynamics Project 2016)

Anisogamy means sexual reproduction by the fusion of dissimilar gametes like sperm (small and motile) and egg cells (large and immotile). The opposite is called isogamy, which is reproduction by the fusion of similar gametes. Anisogamy probably evolved from isogamy, and the question is: why and how?

The lifecycle of primitive plants (such as ferns) has two distinct phases represented by different individuals: the sporophyte and the gametophyte. The sporophyte reproduces asexually by means of spores. Each spore may grow into a gametophyte. The gametophyte reproduces sexually by the production of gametes. Two gametes fuse to form a zygote (=embryo) which grows into a sporophyte, which again reproduces asexually by means of spores, and so on (see figure).



In ferns the sporophyte is tall with big lush leaves, which is the plant you probably have in mind when you think of a fern. The gametophyte is tiny and therefore unknown to most people.

The zygote the product of the fusion of two gametes of sizes x_1 and x_2. The probability of survival of the zygote is an increasing function of its size $z = x_1 + x_2$. The minimum size for zygote survival is $z_{\min} > 0$. If the zygote survives, it produces a sporophyte, which produces spores, half of which carry the allele for x_1 and half the allele for x_2. The gametophytes that develop from these spores produce gametes of a size corresponding to allele inherited from the sporophyte. Assuming that each gametophyte has the same amount of resources, the number of gametes produced is inversely proportional to the gamete size.

Consider a resident population with gamete sizes $x_1, \ldots, x_k$ and corresponding proportions $p_1(t), \ldots, p_k(t)$ in year t. Assuming random pairing of gametes, the proportions of different types of zygotes are

$$q_{ij}(t) = p_i(t)p_j(t)$$

where, for convenience of book-keeping, we use so-called *unordered indexes* with $1 \leq i, j \leq k$. Let $f(z)$ denote the survival probability of a zygote of size z. Then the proportions among the surviving zygotes are

$$r_{ij}(t) = \frac{q_{ij}(t)f(x_i + x_j)}{\sum_{i'=1}^{k} \sum_{j'=1}^{k} q_{i'j'}(t)f(x_{i'} + x_{j'})}.$$

The denominator is merely a normalisation constant so that the $r_{ij}(t)$ sum up to one. The $r_{ij}(t)$ are also the proportions of the different types of sporophytes. Consequently, spores are produced in proportions

$$s_i(t) = \frac{\sum_{j=1}^{k} (r_{ij}(t) + r_{ji}(t))}{\sum_{i'=1}^{k} \sum_{j'=1}^{k} (r_{i'j'}(t) + r_{j'i'}(t))}.$$

Here the denominator is again only for normalisation. The $s_i(t)$ are also the proportions of the different kinds of gametophytes. The *per capita* number of gametes is proportional to the inverse of the size of the gametes. The proportions of gamete types in the next year therefore is

$$p_i(t+1) = \frac{\frac{s_i(t)}{x_i}}{\sum_{i'=1}^{k} \frac{s_{i'}(t)}{x_{i'}}},$$

which, written out in full, becomes

$$p_i(t+1) = \frac{\frac{p_i(t)}{x_i} \sum_{j=1}^{k} p_j(t)f(x_i + x_j)}{\sum_{i'=1}^{k} \sum_{j'=1}^{k} \frac{p_{i'}(t)}{x_{i'}} p_{j'}(t)f(x_i + x_{j'})}$$

Where the denominator is again for normilisatiion.

Study the evolution of gamete size $x \in [0, 1]$ using the theory of adaptive dynamics. Take

$$f(z) = \begin{cases} 1 - e^{-\alpha(z - z_{\min})^2} & \text{if } z > z_{\min} \\ 0 & \text{otherwise} \end{cases}$$

with $z_{\min} = .1$ and $\alpha > 0$.