

The Evolution of Anisogamy

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Anisogamy is the occurrence within a population of two gamete types of different size, a very common condition both in plants and in animals. This paper shows conditions that anisogamy without disassortative fusion (pseudoisogamety) should be favoured by individual natural selection; the results obtained analytically below are in basic agreement with those obtained through the use of numerical techniques by Parker, Baker & Smith (1972). Major results are as follows. First, a necessary condition that gametes of intermediate size should be least fit is that zygote survival should increase more steeply than linearly with zygote size, over at least part of the range of zygote size. Second, stable genetic equilibria involving two alleles may be established, whether these alleles determine gamete size in the haploid or in the diploid phase. Third, if the difference in size between the two gamete types persisting at equilibrium is very great, the two types of gamete-producers will be nearly equally frequent at equilibrium. These results are interpreted to mean that frequency-dependent natural selection may maintain a genetic equilibrium involving two gamete types, provided that the frequency-independent criterion that zygote survival should increase more steeply than linearly with zygote size is satisfied. The importance of zygote size in protists and in multicellular organisms is briefly discussed, but satisfactory quantitative data are lacking. The anisogamy generated in this way is always associated with sexual bipolarity, and an explanation is offered. These arguments lead to the prediction that increasing gamete dimorphism will be associated with increasing vegetative complexity, and a number of phyletic series among the algae, fungi and protozoa were reviewed with this in mind. The Volvocales provide an excellent example of the expected correlation, but other series are less satisfactory. On the whole, the comparative evidence is held to support the predictions of Parker *et al.*, but exceptions to the rule are so numerous that a more detailed examination of the aberrant cases is very desirable.

1. Introduction

Sex has always been an embarrassment to population biologists. The central problem—the identification of an individual selective advantage associated with sexual reproduction—still resists general solution, despite the

best efforts of some of the most able theorists of the day (review in Williams, 1975). Moreover, at least four epiphenomena are widespread amongst sexually reproducing organisms: bipolarity, a nearly equal sex ratio, anisogamy (gamete dimorphism) and somatic dimorphism ("sexual dimorphism"). Surprisingly little attention has been paid to the presence of two and only two sexes, and to the remarkable morphological differentiation of male and female gametes. This paper will attempt to answer the question: why do males and females produce gametes which are so different in size? Light may also be shed on the significance of bipolarity.

Four theories of gamete dimorphism have been proposed. First, Kalmus (1932) and Scudo (1967) show that, under certain plausible conditions, the number of successful fusions occurring in a population is maximal when the gametes are very different in size. [Parker (1971) argues incorrectly that the loss of motility by macrogametes does not affect overall fusion probabilities, and that oogamety has evolved to minimize the total expenditure of energy by the population.] The evolutionary mechanism implied here is a type of group selection, the maximization of the reproductive output of a population. Secondly, Ghiselin (1974) has argued from an economic analogy that gamete dimorphism represents a physiological division of labour, the female gametes specializing in the provision of material for development and the male gametes in motility. Thirdly, Kalmus & Smith (1960) envisage rather similar forces leading to gamete dimorphism via a form of frequency-dependent selection. When large immotile gametes are rare, they will derive an advantage through providing a large store of food for the developing embryo, but this advantage will diminish as they grow more common because of the difficulty of fusion caused by their immotility, and will eventually be lost altogether.

A fourth theory was set out in a remarkable paper by Parker, Baker & Smith (1972; hereafter referred to as PBS). They summarize their major discovery as follows:

"Where zygote fitness is in some way related to zygote volume^x, i.e. to the x th power of zygote volume, relative reproductive rates can be calculated for a range of variants with different gamete productivities (and therefore different gamete sizes). This model yields either drive for small-producing (where the advantage of high productivity exceeds that of increased provisioning for the zygote) or drive for large producing (in the reverse case). However, in certain conditions (over part of the range of x where zygote fitness is proportional to volume^x) a marked disruptive effect can be generated in which the two extremes (large and small gamete production) are favoured."

The selective force involved here is, then, frequency-independent; a necessary condition for the evolution of gamete dimorphism is that the graph of zygote fitness (defined as the overall rate of survival to some unspecified age) on initial zygote size is steeper than linear (has positive second derivatives). When a genetic model involving alternative alleles at a locus was employed, it was found that, when zygote fitness was some appropriate function of zygote size, both alleles continued to segregate in the population indefinitely. This result held whether gamete size were determined in the haploid or in the diploid generation. Moreover, it was also found that if three or more gamete morphs were initially present, only two persisted in the equilibrium population; and, even more surprisingly, if the two persistent types were very different in size, then the two parental types (each parental type producing a different gamete type) were often nearly equally frequent at equilibrium. Finally, PBS pointed out that gamete fitness was also a function of gamete frequency, but did not consider this effect to be an important one. These conclusions are extremely provocative; they offer an interpretation, not only of gamete dimorphism, but also of sexual bipolarity and of the sex ratio. In the present paper, I will attempt to prove by analytical techniques the results obtained by PBS through numerical methods. I will also offer an amended version of their theory, and will attempt to test it using comparative data from protists and thallophytes.

Gametes may differ morphologically, physiologically or behaviourally; gamete differentiation may become apparent either before or during fusion. I will restrict my discussion for the most part to differences in size apparent before fusion, and shall refer to this condition as "anisogamy". However, this usage is not exact. Properly, four types of gamete differentiation should be recognised: isogamety, in which the gametes are equal; pseudoanisogamety, in which they are of different sizes; anisogamety, in which fusion occurs only between gametes of different size; and oogamety, in which fusion occurs only between a very small, usually motile microgamete and a relatively large immotile macrogamete. Further, in gamontogamous protists fusion occurs not between gametes but between gamonts, gamete fusion occurring subsequently in the common space of the aggregated gamont shells; there is then the possibility of isogamonty, anisogamonty, and so forth. However, the gamont seems more nearly analogous to the metazoan soma than to the metazoan gamete, and anisogamonty therefore more nearly analogous to "sexual", i.e. somatic, dimorphism than to gamete dimorphism. I will use the term "anisogamy" indiscriminately to refer to non-isogametous forms of sexual reproduction, except when some more precise usage is required.

The comparative series reviewed below have been abstracted from data presented by Bold (1973), Dittmer (1964), Dogiel (1965), Fritsch (1935),

Grell (1967, 1973), Levine & Ebersold (1960), Lewin (1954), Patrick (1954), Pickett-Heaps (1975), Raper (1954), Scagel *et al.* (1965), Sleight (1973), Smith (1951), Wenrich (1954) and Wiese (1976).

2. A Synthetic Theory of Anisogamy

In this section, the consequences of a simple model of gamete fitness are developed. My intentions are to obtain analytical proofs of the theorems suggested by PBS, and to use these in the construction of a synthetic theory which combines the results obtained by PBS with the ideas of Kalmus & Smith (1960).

(A) CONDITIONS FOR DISRUPTIVE SELECTION ON GAMETE SIZE

Consider a haploid organism which gives rise to haploid gametes. These fuse at random to form diploid zygotes, which persist for some time before dividing meiotically to form a new haploid generation. If anisogamy is to evolve there must be disruptive selection acting on gamete size, such that gametes of intermediate size are least fit. I use the following nomenclature. The gametic type i has an initial frequency p_i ; each type i parent produces n_i gametes each of mass m_i from a fixed mass M of gametic material. The survival (to some unspecified age) of a zygote formed by fusion between a type i and a type j gamete is s_{ij} . The expected survival of zygotes formed by fusions involving type i gametes is thus

$$s_i = \sum_k p_k s_{ik},$$

assuming that fusion occurs at random with respect to gamete type. The "relative reproductive rate" (fitness) of type i parents is clearly $w_i = n_i s_i$, and we can reasonably suppose that $n_i = M/m_i$ approximately. None of this differs substantially from the original model used by PBS. Note that if x_i is the frequency of type i parents, then:

$$p_i = x_i n_i / \sum_k x_k n_k = (x_i / m_i) / \sum_k (x_k / m_k),$$

so that:

$$\partial p_i / \partial m_i = -p_i(1 - p_i) / m_i$$

and

$$\partial p_j / \partial m_i (j \neq i) = p_i p_j / m_i.$$

Necessary and sufficient conditions that there should be disruptive selection on gamete size are that there should exist some value of m_i , namely

m'_i , such that:

$$\left. \begin{array}{l} \text{both } \left. \frac{dw_i}{dm_i} \right|_{m_i = m'_i} = 0 \\ \text{and } \left. \frac{d^2w_i}{dm_i^2} \right|_{m_i = m'_i} > 0 \end{array} \right\} \quad (1)$$

Gamete fitness is affected by gamete size in two ways. First, the production of smaller gametes allows the production of more gametes from a fixed mass of genic material, and other things being equal this tendency will inevitably be favoured by selection. However, a second consideration is that zygote survival may vary directly with zygote size, in which case an increase in gamete mass will increase the expected fitness of individual gametes. Because there is a simple inverse relationship between gamete mass and gamete number, and because gametes of different mass are assumed to be incorporated at random into zygotes, the problem reduces to discovering the relationship between gamete mass and zygote survival which will satisfy conditions (1). Using the model given above, we can replace conditions (1) with equivalent conditions in terms of the effect of gamete mass on zygote survival:

$$\left. \begin{array}{l} \text{both } \sum_k p_k \frac{ds_{ik}}{dm_i} = (1/m'_i) \left[p_i s_{ii} + (1-p_i) \sum_k p_k s_{ik} \right] \\ \text{and } \sum_k p_k \frac{d^2s_{ik}}{dm_i^2} > (2p_i/m'_i) \left[\frac{ds_{ii}}{dm_i} - \frac{s_{ii}}{m'_i} \right] \end{array} \right\} \quad (2)$$

—where all derivatives are evaluated at $m_i = m'_i$. Note that these are not conditions which involve simply the graph of zygote survival on gamete mass, because of the participation of gamete frequencies. However, the simplest situation is nearly frequency-independent. If only the j th gamete type is initially present and then a few i gametes are introduced, we can take $p_i \rightarrow 0$, so that conditions (2) become approximately:

$$\left. \begin{array}{l} \text{both } ds_{ij}/dm_i = s_{ij}/m'_i \\ \text{and } d^2s_{ij}/dm_i^2 > 0 \end{array} \right\} \quad (3)$$

again evaluated at $m_i = m'_i$. Roughly speaking, a population of microgametes may be invaded by macrogametes, and vice versa, if zygote survival increase more steeply than linearly with gamete mass.

This Taylor approximation may not always be realistic. It applies only to genes with small effect, so its use in the case where a single microgamete-producer is introduced into a population of macrogamete-producers (or vice versa) is doubtful. Moreover, it does not always hold if population size is

finite; if a single microgamete-producer arises in a finite population of macrogamete-producers, it may produce so many microgametes that their frequency in the gamete population is immediately appreciable. Conditions (3), therefore, are justifiable only when the difference in size between the two gamete types is relatively small.

Maynard Smith (1978) has derived the conditions for anisogamy to be an evolutionary stable strategy (ESS), using a geometrical argument based on conditions (3).

(B) GENETIC EQUILIBRIUM IN HAPLOID AND DIPLOID MENDELIAN POPULATIONS

To investigate the dynamics of evolutionary change in gamete differentiation, we must harness the results obtained above to a specific genetic model. The choice of models depends on whether gamete size is taken to be determined in the haploid or in the diploid generation; I consider first the haploid case.

Each diploid "sporophyte" gives rise to four (or more) haploid "gametophytes". The fitness of the sporophyte is determined by gamete size through the number and subsequent survival of the gametes produced by the gametophyte, gamete size being determined by the haploid gametophyte genome. The fitness of the ij sporophytes is thus defined to be:

$$w_{ij} = n_i s_i + n_j s_j$$

where

$$s_i = \sum_k p_k s_{ik} = \sum_k n_k x_k s_{ik}$$

(after subsequent cancellation), where p_k is the frequency of the k th type in the gamete population and x_k is the frequency of the k th allele in the gametophyte population. If there are two types (alleles) only, then the fitness of the three sporophyte genotypes are:

$$\begin{aligned} w_{ii} &= 2n_i s_i &= 2x_i n_i^2 s_{ii} + 2(1-x_i)n_i n_j s_{ij} \\ w_{ij} &= n_i s_i + n_j s_j &= x_i n_i^2 s_{ii} + n_i n_j s_{ij} + (1-x_i)n_j^2 s_{ij} \\ w_{jj} &= 2n_j s_j &= 2x_i n_i n_j s_{ij} + 2(1-x_i)n_j^2 s_{jj} \end{aligned}$$

Recasting these equations:

$$\left. \begin{aligned} w_{ij} &= w_{ii} + A \\ w_{ij} &= w_{jj} - A \end{aligned} \right\} \quad (4)$$

where $A = (n_j s_j - n_i s_i)$. The three genotypes have equal fitness if and only if $A = 0$, which occurs when $n_j s_j = n_i s_i$. Substituting for s_j and s_i , this

condition is equivalent to:

$$2x_i n_i n_j s_{ij} + (1 - x_i) n_j^2 s_{jj} = x_i n_i^2 s_{ii} + n_i n_j s_{ij}$$

This equality is satisfied by a single value of x_i , namely \hat{x}_i , given by:

$$\hat{x}_i = (n_i n_j s_{ij} - n_j^2 s_{jj}) / (2n_i n_j s_{ij} - n_i^2 s_{ii} - n_j^2 s_{jj}) \quad (5)$$

Here, \hat{x}_i is an intermediate equilibrium of frequency which is generated by the frequency-dependence of fitness implicit in equations (4), despite the resemblance of equation (5) to the equilibrium frequency reached under frequency-independent selection with overdominance (see Charlesworth, 1978). The equilibrium is stable if:

$$\left. \begin{array}{l} \text{both } w_{ij} > w_{jj} \mid x_i \rightarrow 0 \\ \text{and } w_{ij} > w_{ii} \mid x_i \rightarrow 1 \end{array} \right\} \quad (6)$$

Substituting in equations (4), conditions (6) are equivalent to:

$$\left. \begin{array}{l} \text{both } A < 0 \mid x_i \rightarrow 0 \\ \text{and } A > 0 \mid x_i \rightarrow 1 \end{array} \right\} \quad (7)$$

Define $\theta = m_i/m_j = n_j/n_i$, such that $0 < \theta < 1$, which is equivalent to the arbitrary labelling of the i gametes as microgametes. Further, assume that the relationship between zygote survival and zygote size can be described by $s_{ij} = \alpha m_{ij}^\beta$, as suggested by PBS, where α and β are positive constants and where $m_{ij} \equiv (m_i + m_j)$. Conditions (7) then become:

$$\left. \begin{array}{l} \text{both } 2^{-\beta} \theta^{-1} (1 + \theta)^\beta > 1 \\ \text{and } 2^{-\beta} \theta^{1-\beta} (1 + \theta)^\beta > 1 \end{array} \right\} \quad (8)$$

The upper sentence of conditions (8) gives the maximum value of β for given θ at which microgametes (type i) can invade a population of macrogametes (type j); the lower sentence gives the minimum value of β for given θ at which macrogametes can invade a population of microgametes. If β lies between these two limits, both gamete types will persist in the equilibrium population.

Another result follows from this analysis. In equation (5), substitute $\theta \equiv m_i/m_j = n_j/n_i$, and let $s_{ij} = \alpha(m_i + m_j)^\beta$. The equilibrium frequency of microgamete producers is then given by:

$$x^i = [\theta(1 + \theta)^\beta - 2^\beta \theta^2] / [2\theta(1 + \theta)^\beta - 2^\beta \theta^\beta - 2^\beta \theta^2] \quad (9)$$

Macrogamete-producers will be more frequent than microgamete-producers if $1 < \beta < 2$, while microgamete-producers will be the more frequent if $\beta > 2$. Moreover, besides the trivial case that $\hat{x}_i = \frac{1}{2}$ if $\beta = 2$ exactly, it can be seen that $\hat{x}_i \rightarrow \frac{1}{2}$ as $\theta \rightarrow 0$; that is, the ratio of microgamete-producers

to macrogamete-producers tends to equality as the disparity in size between the two gamete morphs becomes very great. This surprising result (first obtained numerically by PBS) extends the conventional theory of the sex ratio due to Fisher (1930) to the situation in which microgamete-producers and macrogamete-producers are not sexually distinct. It constitutes a novel theoretical observation because the axiom on which the Fisherian theory has been built, that the total of microgamete-producers and the total of macrogamete-producers contribute equally to the next generation, does not hold when microgamete-producers and macrogamete-producers are not sexually distinct.

The problem is slightly more difficult if we imagine gamete size to be determined in the diploid phase. In this case, the initial mass of a zygote depends not on the genotypes of the gametes from which it was formed, but on the genotypes of the diploid parents which gave rise to these gametes. Consequently, retaining the two-allele model leads to the following definitions of fitness:

$$\left. \begin{aligned} w_{ii} &= n_{ii}2s_{i,ii} \\ w_{ij} &= n_{ij}(s_{i,ij} + s_{j,ij}) \\ w_{jj} &= n_{jj}2s_{j,jj} \end{aligned} \right\} \quad (10)$$

The meaning of $s_{i,ii}$ is the expected rate of survival of i gametes produced by ii parents, when incorporated at random into zygotes, i.e.:

$$s_{i,ii} = p_i p_{i,ii} s \left| \begin{matrix} i, ii \\ i, ii \end{matrix} \right| + p_i p_{i,ij} s \left| \begin{matrix} i, ii \\ i, ij \end{matrix} \right| + p_i p_{j,ij} s \left| \begin{matrix} i, ii \\ j, ij \end{matrix} \right| + p_i p_{j,jj} s \left| \begin{matrix} i, ii \\ j, jj \end{matrix} \right| \quad (11)$$

The meaning of $s \left| \begin{matrix} i, ii \\ j, ij \end{matrix} \right|$ is the rate of survival of an ij zygote formed by the fusion of an i gamete from an ii parent with a j gamete from an ij parent. The p_i is the frequency of i gametes in the gamete population; the $p_{i,ii}$ is the frequency of i gametes derived from ii parents in the population of i gametes. The product $p_i p_{i,ii}$ is thus the probability that a given gamete will fuse with an i gamete derived from an ii parent. It can be seen that $p_i p_{i,ii} = n_{ii} x_{ii} / N$, where n_{ii} is the number of gametes produced by ii parents and x_{ii} is the frequency of these parents; $N = n_{ii} x_{ii} + n_{ij} x_{ij} + n_{jj} x_{jj}$ and will cancel in subsequent manipulations. We next observe that gametes derived from diploid individuals of the same genotype have the same mass, ex hypothesi, although they may bear different alleles. If zygote survival varies only with mass, their effects on zygote survival will be identical, so that, for example,

$$s \left| \begin{matrix} i, ij \\ j, ij \end{matrix} \right| = s \left| \begin{matrix} j, ij \\ j, ij \end{matrix} \right| \equiv s \left| \begin{matrix} ij \\ ij \end{matrix} \right|.$$

Using this principle, we can substitute into equation (11) to obtain:

$$\left. \begin{aligned} s_{i,ii} &= n_{ii}x_{ii} s \left| \frac{ii}{ii} \right| + n_{ij}x_{ij} s \left| \frac{ii}{ij} \right| + n_{jj}x_{jj} s \left| \frac{ii}{jj} \right| \\ s_{i,ij} &= n_{ii}x_{ii} s \left| \frac{ij}{ii} \right| + n_{ij}x_{ij} s \left| \frac{ij}{ij} \right| + n_{jj}x_{jj} s \left| \frac{ij}{jj} \right| \\ s_{j,ij} &= s_{i,ij} \\ s_{j,jj} &= n_{ii}x_{ii} s \left| \frac{jj}{ii} \right| + n_{ij}x_{ij} s \left| \frac{jj}{ij} \right| + n_{jj}x_{jj} s \left| \frac{jj}{jj} \right| \end{aligned} \right\} (12)$$

If the *i* allele is dominant, we can suppose that *ii* and *ij* individuals produce gametes of mass θm , whilst *jj* individuals produce gametes of mass m , where $0 < \theta < 1$ as before. Further, suppose that zygote survival varies with zygote mass as in the haploid model above. Then substitution in equation (12), and substitution of the results into equation (10), yields:

$$\left. \begin{aligned} w_{ii} &= (\alpha M m_j^{\beta-2}) [\theta^{-1}(1+\theta)^\beta (x_{ii}+x_{ij}) + 2^\beta x_{jj}] \\ w_{ij} &= w_{ii} \\ w_{jj} &= (\alpha M m_j^{\beta-2}) [2^\beta \theta^{\beta-2} (x_{ii}+x_{ij}) + \theta^{-1}(1+\theta)^\beta x_{jj}] \end{aligned} \right\} (13)$$

Solving for $w_{ii} = w_{ij} = w_{jj}$ yields an equilibrium frequency of microgamete-producers:

$$\widehat{(x_{ii}+x_{ij})} = [\theta(1+\theta)^\beta - 2^\beta \theta^2] / [2\theta(1+\theta)^\beta - 2^\beta \theta^2 - 2^\beta \theta^2] \quad (14)$$

Clearly, there will be an intermediate equilibrium frequency with $0 < \widehat{(x_{ii}+x_{ij})} < 1$ if conditions (8) apply. The equilibrium can be shown to be stable by noting that:

- (1) $w_{ij} > w_{jj} \mid x_{ii} \rightarrow 0$ |, if $(x_{ii}+x_{ij}) < \widehat{(x_{ii}+x_{ij})}$, and
- (2) $w_{jj} > w_{ij} \mid x_{ii} \rightarrow 1$ |, if $1 - (x_{ii}+x_{ij}) < 1 - \widehat{(x_{ii}+x_{ij})}$.

The dynamics of selection are thus directly analogous with the haploid case analysed above. Moreover, it is again true that $\widehat{(x_{ii}+x_{ij})} \rightarrow \frac{1}{2}$ as $\theta \rightarrow 0$. The same conclusions hold if the *i* allele is recessive. There are, then, no substantial differences between the conclusions drawn from haploid and from diploid models. Charlesworth (1978) has presented an alternative account of haploid and diploid models, from which he draws the same conclusions.

(C) THE SYNTHETIC THEORY

The arguments developed above allow the model of PBS to be reconciled with that of Kalmus & Smith (1960) within a synthetic theory of the evolution of anisogamy. The fitness (survival) of a given zygote type is independent of

the frequencies of the gamete types, being determined by the combined mass of the fusing gametes only. Nevertheless, the overall fitness of gametes is frequency-dependent, since the sizes of zygotes into which gametes of a given type are incorporated varies with the frequencies of all types in the gamete population. A graph of zygote survival on zygote size which increases more steeply than linearly is always a necessary condition for the evolution of anisogamy, but it is sufficient only when the effects of frequency can be neglected [conditions (3)]. When two or more alleles governing gamete size are segregating with appreciable frequency in the population, the effects of frequency cannot be discounted [conditions (2)], and the equilibrium of two alleles is governed by the frequency-dependence of gamete fitness [expressions (4) through (8)].

These arguments provide an interpretation of the three major results obtained numerically by PBS, concerning the generation of disruptive selection for gamete size, the maintenance of a stable genetic equilibrium and the equal frequency of the two persisting types in extreme anisogamy.

3. General Features of the Models

(A) GENETIC DETERMINATION OF GAMETE SIZE

All the models used above assume as a matter of course that gamete size is inherited. In fact, both sexuality and gamete differentiation may be under environmental control, as in at least some of the endoparasitic Coccidia. However, they are usually determined by a simple Mendelian mechanism. This involves the segregation of alternative alleles during a postzygotic meiosis in many dioecious protists and thallophytes; in higher organisms, the segregating elements are commonly entire chromosomes, gamete size being determined prior to gametogenesis. An acceptable generalization seems to be, that gamete size is determined in the haploid phase of organisms with haploid-homophasic life cycles, and in the diploid phase of organisms with diploid-homophasic cycles.

(B) GAMETE FUSION

Strictly speaking, the models require that freeswimming gametes should unite at random with respect to gamete size. This requirement is probably nearly met by pseudoanisogametous protists. However, in the majority of sexually reproducing organisms, departures from random fusion are introduced by disassortative fusion and by differential motility.

In anisogametous (as opposed to pseudoanisogametous) forms, the gamete morphs are sexually distinct. It is a remarkable fact that sexuality in

morphologically anisogamous forms is invariably bipolar, in contrast with the multipolar sexuality of some ciliates and fungi. Part of the explanation may be as follows. A necessary condition that there should be a stable equilibrium involving two gamete morphs is that the curve of zygote survival on zygote size should contain a region with positive second derivatives. If there are to be three gamete morphs which represent locally stable equilibria, then the curve must contain two separate regions with positive second derivatives, and so forth. The increasing complexity of the curves necessary to sustain more than two gamete morphs lacks empirical support, nor is it clear what biological forces could be involved in generating curves which possess more than one region with positive second derivatives. The evolution of three or more gamete types which are both sexually and morphologically distinct is therefore unlikely, although this argument does not preclude sexual differentiation within either of the two gamete types. But consider a population which has evolved a fairly pronounced degree of anisogamy, with two morphologically distinct gamete morphs. Assortative fusion is unlikely to be tolerated because microgamete-to-microgamete fusion will be lethal or nearly so, whilst macrogamete-to-macrogamete fusion is improbable because of the loss of motility of the macrogametes. Sexual differentiation which restricts fusion to within gamete types is therefore unlikely, and is in fact not found in anisogameteous chlorophyte algae (Wiese, 1976). A final possibility remains: sexual differentiation within both gamete types accompanied by disassortative fusion with respect to gamete size. For instance, there might be the two sexes *A* and *B* amongst microgametes, corresponding to the macrogamete sexes *A'* and *B'*; only $A \times A'$ and $B \times B'$ fusions produce viable zygotes. There appear to be two difficulties with this scheme. First, the evolutionary process is difficult to envisage: if only the *A* and *A'* sexes were initially present, and the *B* sex then appeared amongst the microgametes, how could members of the *B* sex reproduce unless the *B'* sex appeared simultaneously amongst the macrogametes? Even if this were to happen, the fitnesses of the two minority sexes would vary directly with their frequencies and would be very low when both were rare because of the improbability of encountering a compatible partner. Thus, once anisogamy has evolved, sexual differentiation within either gamete type is unlikely to occur, and the sexual bipolarity of the population is conserved. These difficulties do not apply to isogametes, and multipolar mating systems are to be expected only in isogamous populations.

The appearance of disassortative fusion invalidates the assumption that gametes fuse at random, but PBS argue convincingly that anisogamety has evolved from pseudoanisogamety, and is contingent on the prior evolution of morphological differences among sexually undifferentiated gametes. They

invoke a form of sexual selection in which microgamete producers are always able to break down the defences against disassortative fusion more rapidly than the macrogamete producers are able to erect them, because of the greater selection differential acting on them and because of the greater numbers and consequently greater genetic variability of microgametes relative to macrogametes. Oogamety then tends to evolve from anisogamety because of selection for immotility amongst macrogametes, to obviate expenditure of energy in locomotion, and for motility among microgametes, to increase the probability of fusion. The comparative evidence for the derived nature of anisogamety and oogamety is reviewed below.

(C) ZYGOTE FITNESS AND ZYGOTE SIZE

The disruptive selection of gamete size requires that the graph of zygote fitness on zygote size be steeper than linear, at least over part of the range of zygote size. There appears to be no direct evidence on this point, either from protists or from metazoans. Among anamniote vertebrates, zygote size is known to influence the course of the life history in various ways, for example by altering developmental rates and larval size and growth [see, for example, a review of urodeles by Salthe (1969) and of anurans by Salthe & Duellman (1973)]. Amongst invertebrates, Lawler (1976) showed that older female *Armadillidium* (Oniscoidea) produce smaller eggs which are more liable to developmental failure before hatching; the correlation between smaller egg size and an increased rate of developmental failure continued to hold within the oldest age group. Moreover, he suggested that egg size may also affect the survival of young after hatching, and even (via the magnification of small size differences at hatching, by exponential growth) their subsequent fecundity. Large eggs appear to be much less susceptible to predation by other invertebrates in certain freshwater crustaceans (Belk, 1977; Kerfoot, 1974). Unfortunately, it is difficult to assess these effects quantitatively.

Blaxter & Hempel (1963) found that the time taken for 50% of samples of starved herring larvae to die in the laboratory was an increasing linear function of egg weight. This suggests, but does not prove, that in these samples the rate of survival to given age is an increasing curvilinear function of egg weight.

Egg diameter is a curiously invariable trait among anamniote vertebrates, the entire range of variation spanning only about one order of magnitude (reviews and data in Marshall, 1953; Turner, 1962; Salthe, 1969; Salthe & Duellman, 1973; Scott & Crossman, 1973; Ware, 1975). The smallest eggs are produced by various gobies among the teleosts (0.3–0.4 mm; the agnathan *Lampetra* has eggs of about 0.65 mm diameter), by *Bufo* and *Hyla* among anurans (0.8–1.0 mm) and by *Ambystoma* among urodeles (1.2 mm).

With the exception of elasmobranchs, the largest eggs are those produced by the zoarcid *Austrolycichthys* and by salmonids such as *Salmo* and *Oncorhynchus* among the teleosts (5–7 mm), by *Ascaphus* and *Barbourella* among anurans (about 5 mm) and by *Andrias* among the urodeles (about 7 mm). Almost all anamniote eggs, therefore, fall in the range of 0.5–5.0 mm diameter. This paucity of variation is especially striking when contrasted with the variation in egg number, which spans about nine orders of magnitude from the single egg produced by the leptodactylid *Sminthillus* to the 10^9 eggs of the ocean sunfish *Mola*, with many forms producing between 10^2 and 10^6 per breeding season. The low variability of egg size, relative to egg number, is also a general phenomenon within populations of the same species (Ware, 1975). Egg size, therefore, seems to be under rather strict selective control. In addition, there seems to be a ban on eggs of smaller than about 0.5 mm diameter, and it seems reasonable to suggest that eggs which are any smaller than this are incapable of normal development, at least in the groups surveyed. Likewise, very few eggs are larger than about 5 mm diameter and this may be the point, for most species, at or below which any further increase in egg size is bound to be unprofitable, relative to a corresponding increase in egg number. These observations suggest that the graph of zygote survival on zygote size is sigmoidal, survival being essentially zero below 0.5 mm diameter, thereafter increasing with zygote size, but reaching an asymptote before 5 mm diameter. A region with positive second derivatives would exist in the left-hand part of such a curve.

In some anisogamous protists, unfertilized egg cells can transform into parthenospores, which resemble zygotes and germinate under the same conditions. This has been observed both in anisogametous (e.g. *Volvox aureus*, Grell, 1973) and in anisogamontous protozoans (e.g. *Vorticella*, Finley, 1939), in various algae including the oogametous *Oedogonium*, and in the fungal genera *Allomyces* and *Achlya* (Raper, 1954). Microgametes and microgamonts do not have this capacity, but degenerate and die if they do not achieve fusion. These observations appear to confirm the importance of zygote size in unicellular and the lower multicellular organisms.

4. Gamete Dimorphism and Vegetative Complexity

Whilst multicellular organisms are usually anisogamous, unicellular organisms often produce isogametes. PBS interpret this difference as follows. The critical factor in the evolution of anisogamy is the relationship between zygote survival and zygote size. Multicellular organisms require a zygote sufficiently large to contain the energy reserves necessary to fuel increase in size and morphological differentiation; unicellular organisms, on the

other hand, are essentially "gametic adults", and display little increase in size or differentiation after fusion. Thus, zygote size may be critically important to the survival of the eggs of multicellular organisms, whilst zygote number will be the prime determinant of fitness in unicellular animals and plants. The expected trend is therefore towards gametic differentiation in morphologically complex organisms, and towards gamete smallness in the simplest organisms. This correlation of the degree of gamete dimorphism with the degree of vegetative complexity should be apparent, not only at the gross level mentioned above, but for any comparative series in which a transition between isogamy and anisogamy is observed.

The most extensive comparative series exist in the Algae, where a correlation between gamete dimorphism and vegetative complexity has often been noted; for example, Fritsch (1935, p. 43) says "Certain it is that oogamy is confined to those classes that exhibit the highest vegetative differentiation, sexual reproduction where it occurs in the others being always isogamous." There is no difficulty in confirming this observation on the broadest taxonomic level (Table 1). The largest and most complex vegetative structures are found among the Phaeophyceae and Rhodophyceae, and amongst the Charales (Charophyta) and certain other Chlorophyceae. These are typically oogametous groups, although isogamy is reported for some Phaeophyceae and is widespread in siphonous Chlorophyceae. On the other hand, most unicellular forms (Chrysophyceae, Bacillariophyceae, Cryptophyceae, Dinophyceae) are isogamous, although anisogamy is well known from the unicellular Chlorophyceae. Amongst the Algae as a whole, then, there is a tendency for the transition from isogamy to anisogamy to be associated with the transition from simple to complex vegetative structure; but there are certain exceptions to this rule, chiefly amongst the Chlorophyceae.

Narrowing the field, we can examine variation at the family level amongst the Chlorophyceae. Unicellular representatives of Volvocales, Chlorococcales and Conjugales tend to be isogamous as expected, but again with certain conspicuous exceptions, especially in the Volvocales. The Ulotrichales, Cladophorales and Chaetophorales are of intermediate structural complexity, and include forms which span the entire range from isogamy to well-defined oogamety. The most advanced forms are found amongst the Oedogoniales, Siphonales and Charales, and are typically anisogametic or oogametic, but with isogamy in many groups of the Siphonales. A more rigorous approach is to identify lines of evolution within the Chlorophyceae, and then to characterize the mode of reproduction of forms of increasing size and differentiation within these lines. In the discussion which follows, I have followed Scagel *et al.* (1965) in separating the volvocine, tetrasporine and siphonous tendencies.

TABLE 1

A summary of vegetative complexity and gamete differentiation in the Algae

Family	Size	Form	Division of Labour:					Gametes
			ATT	LOC	NUT	REP	VEG	
Volvocales:								
Chlamydomonadaceae	1,2	1,2,3	0	0/+	0	0/+	0	I, PA, A, O
Sphaerellaceae	1,2,3	1,3	0	+	0	+	0	I, A, O
Polyblepharidaceae	1	1,2	0	0	0	0	0	I, PA
Phacotaceae	1	1	0	0	0	0	0	I
Tetrasporaceae	1 to 5	2	0/+	0	0	0	0	I
Palmellaceae	1 to 5	2	0	0	0	0	0	I
Chlorodendraceae	1,2,3	1,2,5	+	0	0	+	0	I
Chlorococcales:								
Chlorococcaceae	1	1	0	0	0	0	0	I, PA, A
Eremosphaeraceae	1	1	0	0	0	0	0	I
Chlorellaceae	1,2	1,2	0	0	0	0	0	?I, O
Hydrodictyaceae	2,3,4,5	2,3	0	0	0	0	0	I, PA or A
Coelastraceae	2	3	0	?+	0	0	0	?I
Ulotrichales:								
Ulotrichaceae	4	4	+	0	0	0	?+	I
Microsporaceae	4	4	0	0	0	0	0	I, ?PA
Cylindrocapsaceae	4	4	+	0	0	+	0	O
Ulvaceae	5	5	+	0	0	0/+	+	I, PA, A
Prasiolaceae	4	5	0/+	0	0	+	0	A
Sphaeropleaceae	4	4	0	0	0	0	0	O
Cladophorales:								
Cladophoraceae	4,5	4,5	0/+	0	0/+	0	+	I, A
Chaetophorales:								
Chaetophoraceae	4	5,6	+	0	+	+	+	I, O
Trentepohliaceae	3,4	5	+	0	0/+	0	+	I, ?A
Coleochaetaceae	4	5,6	+	0	0/+	+	+	O
Pleurococcaceae	1,2	1,2	0	0	0	0	0	asexual
Oedogoniales:								
Oedogoniaceae	4	4,5,6	+	0	+	+	+	O
Conjugales:								
Mesotaeniaceae	1,2	1,2,4	0	0	0	0	0	I (conjugation)
Zygnemaceae	4	4	0/+	0	0	0	0	I, A (conjugation)
Mongeotiaceae	4	4	0/+	0	0	0	0	I, A (conjugation)
Desmidiaceae	1 to 5	1 to 4	0	0	0	0	0	I (conjugation)
Siphonales:								
Protosiphonaceae	4	1	+	0	+	0	0	I, PA, A
Caulerpaceae	4,5	6,7	+	0	+	+	+	A
Derbesiaceae	5	6	+	0	+	+	+	PA or A
Dasycladaceae	5	7	+	0	+	+	+	I, PA or A
Codiaceae	4,5	7	+	0	+	+	+	A
Valoniaceae	4	1	+	0	+	+	+	I
Chaetosiphonaceae	3,4	4,5	+	0	+	+	+	?
Vaucheriaceae	5	5,6	+	0	+	+	+	O

TABLE 1—*continued*

Family	Size	Form	Division of Labour:					Gametes
			ATT	LOC	NUT	REP	VEG	
Charales:								
Characeae	5	7	+	0	+	+	+	O
Xanthophyceae	3-4	4	+	0	+	+	+	I, A
Chrysophyceae	1	1	0	0	0	0	0	I
Bacillariophyceae	1	1	0	0	0	0	0	I, A, O
Cryptophyceae	1	1	0	0	0	0	0	I
Dinophyceae	1	1	0	0	0	0	0	I
Chloromonadineae	1	1	0	0	0	0	0	?
Euglenineae	1,2	1,2	0	0	0	0	0	asexual
Phaeophyceae	5	5-7	+	0	+	+	+	I, A, O
Rhodophyceae	5	7	+	0	+	+	+	O

Size 1: unicellular. 2: 2-10² cells in colony. 3: 10²-10⁴ cells in the colony; microscopic coenocytes. 4: macroscopic colonies, to 1 cm; several cm of simple filament; macroscopic coenocytes. 5: macroscopic, greater than 1 cm, several cells thick.

Form. 1: unicellular, motile or coccoid. 2: colonial, non-coenobial; palmelloid. 3: colonial, coenobial. 4: simple filaments. 5: branched filaments; parenchymatous thallus. 6: heterotrichous. 7: advanced heterotrichous forms.

Division of labour: Provision of specialized cells for the following functions. ATT: attachment; specialized rhizoids or basal organs. LOC: locomotion (only in motile coenobia; not including motile swarms or gametes). NUT: nutrition. REP: sexual or asexual reproduction, gametangia and sporangia. VEG: vegetative growth, including fragmentation; e.g. apical cells.

Gametes: I: isogamety. PA: pseudoanisogamety. A: anisogamety. O: oogamety.

The classification adopted here follows Fritsch (1935), since his account was the source for most of the data. More recent authorities, for example Pickett-Heaps (1975) and Stewart & Mattox (1975) have advocated rather different phylogenies; the only purpose of the material above, however, is to summarize variation at the level of the family. In particular, *Vaucheria* is now included in the Xanthophyceae, and the Charales have been removed from the Chlorophyceae into a group of their own.

To increase the range of forms represented, I have extended the volvocine series to include the whole of the Volvocales [Table 2(a)]. Within the family, a clear trend emerges. Unicellular and palmelloid species are usually isogamous, although a few species of the unicellular genera *Chlamydomonas*, *Carteria* and *Chlorogonium* are anisogamous and may even be oogametic. Noncoenobial colonial forms are intermediate in structural complexity, and are isogametic (*Raciborskiella*) or pseudoanisogametic (*Dangeardinella*). Finally, the advanced coenobial forms show a high proportion of oogametic species; they grade from the simplest 4-16 cell isogametic *Pyrobotrys* and *Stephanosphaera* to the advanced oogametic species of *Volvox*, where the colony may comprise in excess of 50 000 cells. *Gonium* and *Pandorina*, which are intermediate in size and complexity, are also intermediate in gamete

differentiation, showing anisogamy without disassortative fusion. Besides providing support for the main thesis advanced by PBS, this series is also consistent with the notion that disassortative fusion and true oogamety are derived from a primitive pseudoanisogamety in vegetatively less complex forms. The significance of the Volvocales has been noticed by a number of previous authors, including Knowlton (1974).

The other two chlorophyte series are considerably less convincing. In the tetrasporine line [Table 2(b)], unicellular, filamentous and the less advanced heterotrichous genera are usually isogamous, but *Cylindrocapsa* presents a puzzling exception in which a simple filamentous habit is associated with oogamety. Moreover, those genera of the Chaetophorales in which the erect system is suppressed are commonly oogametic, despite their relatively

TABLE 2

Representative genera in three phyletic series of chlorophyte algae, to show the relationship between vegetative structure and gamete dimorphism. Discussion in text; authorities cited in Introduction

2(a) *The volvocine series, interpreted as the Volvocales*

Genus	Structural grade	Gamete differentiation	
<i>Lobomonas</i>	} Unicellular	Isogamy	
<i>Sphaerella</i>			
<i>Dunaliella</i>			
<i>Polytomella</i>			
<i>Carteria</i>			
<i>Chlorogonium</i>	} Unicellular	Usually isogamous, some oogametous forms.	
<i>Phyllomonas</i>	} Unicellular		
<i>Chlamydomonas</i>			Isogamy (over 40 spp.); pseudoanisogamety; anisogamety (11 spp.); oogamety (3 spp.).
<i>Apiocystis</i>	} Palmelloid colonies	Isogamy	
<i>Tetraspora</i>			
<i>Palmella</i>	} Non-coenobial colony, 2 ¹ -2 ⁴ cells	Isogamy	
<i>Raciborskiella</i>		Pseudoanisogamety	
<i>Dangeardinella</i>		Isogamy	
<i>Pyrobotris</i>		Coenobium, 2 ² -2 ⁴ cells	Isogamy
<i>Stephanosphaera</i>		Coenobium, 2 ³ cells	Isogamy or pseudoanisogamety
<i>Gonium</i>		Coenobium, 2 ⁴ cells	Pseudoanisogamety
<i>Pandorina</i>		Coenobium, 2 ⁴ cells	Anisogamety
<i>Platydorina</i>	Coenobium, 2 ⁵ cells	Oogamety	
<i>Eudorina</i>	Coenobium, 2 ⁴ -2 ⁶ cells	Oogamety	
<i>Pleodorina</i>	Coenobium, 2 ⁷ cells	Oogamety	
<i>Volvox</i>	Coenobium, more than 20 000 cells	Oogamety	

TABLE 2—*continued*2(b) *The tetrasporine series*

Genus	Structural grade	Gamete differentiation
<i>Chlorococcum</i>	Unicellular	Isogamy
<i>Tetraspora</i>	Large palmelloid colony of undifferentiated cells	Isogamy
<i>Cylindrocapsa</i>	Simple uniseriate filament	Oogamy
<i>Microspora</i>	Simple uniseriate filament with slightly differentiated basal cell	Isogamy
<i>Ulothrix</i>	Simple uniseriate filament with basal holdfast	Isogamy
<i>Stigeoclonium</i>	Primitive heterotrichy; branched uniseriate filament attached by rhizoids	Isogamy
<i>Chaetopeltis</i> , etc.	Several primitively heterotrichous genera with erect system completely or almost completely suppressed	Isogamy
<i>Aphanochaete</i>	Erect system represented by a few hairs only	Oogamy
<i>Chaetonema</i>	Erect system represented by a few branches only	Oogamy
<i>Draparnaldia</i>	Large-celled main filament with many outgrowths of branching small-celled filaments; basal system suppressed	Isogamy
<i>Monostroma</i>	Monostromous thallus formed by repeated cell division in second plane	Anisogamy
<i>Ulva</i>	Foliose thallus, cells divide once in third plane, with basal holdfast; to 30 cm.	Isogamy; slight anisogamy in some species
<i>Enteromorpha</i>	Large tubular thallus, otherwise similar to <i>Ulva</i>	Anisogamy; isogamy in some species
<i>Fritschiella</i>	Partially parenchymatous thallus produced by repeated divisions in third plane; advanced heterotrichy but plant body microscopic	Isogamy

2(c) *The siphonous (multinucleate) series*

Genus	Structural grade	Gamete differentiation
<i>Protosiphon</i>	Unicell with green aerial and colourless rhizoidal parts (rhizoid to 1 mm)	Isogamy
<i>Valonia</i>	Immense unicell (to 5 cm), perhaps divided without crosswalls	Isogamy

TABLE 2—continued

(2c)—continued

Genus	Structural grade	Gamete differentiation
<i>Pediastrum</i>	Discoid coenobium, outer cells spinose	Isogamy
<i>Chaetomorpha</i>	Simple uniseriate filament	Isogamy
<i>Urospora</i>	Simple uniseriate filament	Slight anisogamy
<i>Sphaeroplea</i>	Simple uniseriate filament	Oogamy
<i>Rhizoclonium</i> (= <i>Lola</i>)	Simple or sparsely branched uniseriate filament	Slight anisogamy
<i>Hydrodictyon</i>	Filamentous network	Isogamy
<i>Cladophora</i>	Dense mat of branched uniseriate filaments attached by rhizoids	Isogamy
<i>Halicystis-Derbesia</i>	Gametophyte a spherical thallus attached by rhizoids; sporophyte a branched coenocytic tube	Anisogamy
<i>Bryopsis</i>	Delicately and profusely branched filaments borne on naked stem arising from rhizome, attached by rhizoids	Anisogamy
<i>Caulerpa</i>	'Leaves' borne on main shoots more complex than in <i>Bryopsis</i>	Anisogamy
<i>Dasycladus</i>	Unbranched main shoot (to 5 cm) arises from richly branched rhizoid and bears dense alternating whorls of green tissue	Isogamy
<i>Codium</i>	Profusely branched filaments form massive parenchymatous thallus	Anisogamy

simple structure and small size. In the more complex Ulvaceae the expected anisogamy is observed, but the advanced parenchymatous structure found in *Fritschiella* is associated with isogamy; the plant body of this genus is quite small, however.

Siphonous forms [Table 2(c)] also show the expected trend whilst including conspicuous exceptions. Unicellular and filamentous genera are commonly isogamous, but the filamentous *Sphaeroplea* has oogamy. More complex forms are usually anisogamous but the relatively large and advanced genus *Dasycladus* has isogamy.

In short, the Algae show a tendency for isogamy to be associated with simplicity of vegetative structure, no matter at what phylogenetic level the comparison is made. This argument is weakened by the existence of isogamous but vegetatively complex forms (for example, Dasycladaceae), and of structurally simple but oogametic forms (for example, certain species of unicellular Volvocales). One critical test of theory might be performed within

the genus *Chlamydomonas*, where a few anisogamous species are found amongst a large number of isogamous and asexual forms. Non-isogamous sexual species should display some unusual degree of dependence on initial zygote size, and in fact there is a hint that this dependence may exist. The differentiation of gametes from vegetative cells may occur in two basic ways: either all haploid cells are potential gametes, or the potential for fusion is restricted to smaller cells, sexual activity being lost as the cell enlarges prior to asexual division. The isogamous species of *Chlamydomonas* and members of the isogamous genera *Polytoma* and *Dunaliella* belong to the first group; non-isogamous species of *Chlamydomonas* and *Chlorogonium* belong to the second. This supplies the necessary hint that anisogamy will evolve whenever there is a premium on large zygote size created by the necessity of postzygotic growth.

The remaining groups of algae offer some additional support. Pyrrhophyta (Dinophyceae) are only occasionally sexual. *Ceratium* is reported to undergo a sort of conjugation, the two gametic protoplasts migrating along a tube joining the two cells in order to fuse. There is external fusion in *Gymnodinium*, where the gametes are isogamous. Both genera are unicellular.

There is some variation in gamete differentiation within the Xanthophyceae. *Tribonema* is an unbranched filamentous genus with occasional sexual reproduction; the gametes are of equal size, but the "male" gamete is motile whilst the "female" is not. *Botrydium* consists of a small (2 mm) globose coenocytic thallus attached by a fairly complex system of rhizoids; some species are isogamous and some anisogamous. *Vaucheria* is a branched coenocytic filament, and is oogamous.

The Chrysophyceae are mostly motile unicells, with some colonial and a very few filamentous forms. When sexual reproduction occurs it seems always to be isogamous, even in the colonial genus *Dinobryon*. The Bacillariophyceae (diatoms) are also predominantly unicellular, with a few filamentous and colonial forms. Sexual reproduction is characteristically isogamous, or involves gametes of different motility but equal mass, but Patrick (1954) describes a distinct oogamy in *Melosira* and *Cyclotella*. It is interesting that neither genus is unicellular in habit, *Melosira* being filamentous and *Cyclotella* colonial.

The Phaeophyceae (brown algae, "seaweeds") are predominantly isogamous, but the few isogamous forms tend to be vegetatively simple. *Ectocarpus* and *Sphacelaria* have a tuft-like habit, the small plants being much-branched filaments arising from a prostrate rhizoid. They have an isomorphic alternation of generations, and are isogamous (a slight tendency to anisogamy is reported from one species of *Sphacelaria*). *Zanardinia* is a small flat expanded thallus; it has an isomorphic alternation of generations and is

distinctly anisogamous. The related *Cutleria* has a heteromorphic alternation, the sporophyte resembling *Zanardinia* but the gametophyte being an erect flattened thallus elaborated by repeated dichotomous branching, and this advance in structural grade is accompanied by oogamy. Forms in the more advanced orders Dictyotales, Laminariales and Fucales include the typical brown seaweeds, characteristically with a large dissected bladelike thallus attached to a basal holdfast by a stipe, and with pronounced heteromorphic alternation of generations, the gametophyte being eventually (e.g. in *Fucus*) represented only by the gametes; all these large and vegetatively complex forms are oogamous.

The mode of sexual reproduction shows a correlation with the life cycle, as well as with the degree of vegetative complexity. Chlorophyte algae with an isomorphic alternation of generations are almost invariably isogamous, although the slight anisogamy reported for *Enteromorpha* appears to be an exception. Forms with a heteromorphic alternation, such as *Halicystis*—*Derbesia*, appear to be anisogamous. True oogamy is found only in genera with haploid-homophasic cycles, that is, cycles in which the only diploid stage is a more or less transient zygote. These trends are to some extent independent of trends in morphological differentiation and the synthetic theory advanced above does not seem to provide any basis for interpreting them. The phenomenon is confined to the chlorophytes, however; most rhodophytes have an isomorphic alternation, but all are oogametic.

Phyletic series in gamete differentiation are not as well documented or as extensive in the Fungi as in the Algae, and the fusion of freeswimming gametes occurs only in three orders of primitive and vegetatively simple phycomycetes. The Chytridiales are the most primitive of the three; they are endoparasitic unicells with isogamy. The Blastocladiales includes both isogamous and anisogamous forms, both microgametes and macrogametes being motile when they occur. The Monoblepharidales are oogametic, with an immotile macrogamete. The more advanced fungi which produce distinct gametic cells are invariably oogametic. Again, the association of isogamy with the unicellular habit is striking.

Among the Protozoa, several groups contain isogamous forms, including the Phytomonadina (= Volvocales), reviewed above in the chlorophyte algae. In the Polymastigina, haploid-homophasic genera are gametogamous (with autogamy as an alternative); most are isogamous, but anisogamy is reported for *Eucomonympha*, and there is a distinct structural difference between the like-sized gametes of *Trichonympha*. Autogamous and gamontogamous genera are isogametic and isogamontic. Two diploid genera of Heliozoa reproduce sexually; both are autogamous with isogamety. The Foraminifera are heterophasic, with a haploid gamont. All gametogamous

forms are isogametic, producing motile microgametes only. Amongst gamontogamous forms, *Rubratella* has differentiated gametes and gamonts, but without disassortative fusion. The sporozoa are haploid-homophasic with a zygotic meiosis. The gamontogamous gregarines range from isogamety to oogamety, in the latter case with disassortative fusion. *Stylocephalus* is very unusual in that the motile gamete is the larger. The Coccidia are all oogametic; Adeleidae are in addition anisogamontic. Although some of the taxa mentioned above include both isogamous and anisogamous forms, they are of little use for comparative tests of theory, since all the organisms are unicellular. Some slight support for the present theory is given by the remaining group, the Ciliata, which are diplonts with a gametic meiosis and gamontogamous "conjugation". The majority of ciliates are unicellular and isogamontic, but the peritrichs have a unilateral anisogamontic fertilization. This is suggestive, since many peritrichs are colonial, but on the other hand both unicellular and colonial forms have differently sized gamonts. However, in solitary forms the gamonts are formed by a differential division generating two unequal protoplasts, whereas in colonial genera the microgamonts are relatively smaller, and are formed by the repeated division of a single cell. The macrogamonts are stalked and sessile whilst the microgamonts are freeswimming, so there is a close analogy between the peritrich gamont and the gametes of other organisms.

PBS also speculate that oogamety is a derived condition, resulting from the specialization of microgametes for motility (to increase the probability of fusion) and the specialization of macrogametes for immotility (to conserve energy), and contingent on the prior evolution of pseudoanisogamety. This view does not seem essentially different from the theory advanced independently by Ghiselin (1974). The comparative evidence favours the theory, in that oogamety tends to be associated with the most advanced structural grade in the series reviewed above. Leaving aside the exceptions to this rule, however, two uncomfortable objections remain. First, selection for microgamete motility should be least when gamete fusion is spatially constrained in some way, and yet the microgamete is active in internally fertilized metazoa and the microgamont in gamontogamous protozoans. Perhaps sexual selection resulting from competition between sperm can be invoked to explain the persistence of motile microgametes in internally fertilized metazoa, even in those cases where the sperm are retained in spermathecae and their access to the eggs controlled by the female. In peritrichs, it is interesting that both sessile and freeliving forms are anisogamontous, but there are conspicuous differences in gamont size before fertilization only in sessile forms. The second difficulty is that selection for microgamete motility should be greatest when the microgametes are released into the

external medium, and yet there are obvious exceptions to this rule. In the case of pollen grains, it can be argued that size and motility come to the same thing; the smaller the male gamete, the more widely dispersed it will be. The interpretation of the amoeboid microgametes of all Rhodophyta is less obvious.

This brief review of gamete differentiation on protists tends to confirm the prediction offered by PBS as a test of their conclusions, that increased vegetative size and complexity should be accompanied by the development of anisogamy. To this extent the theory is supported, but two reservations must be made. The first is that the crucial contribution of increased size to the survival and differentiation of the zygotes of multicellular organisms has not been adequately investigated, however reasonable a supposition it might appear to be. The second is that numerous exceptions to the rule have been pointed out: on the one hand, there are vegetatively simple and even unicellular forms as in the Volvocaceae and the Micractiniaceae, which are fully oogamous, whilst on the other hand there are large and vegetatively complex forms such as *Ulva* and *Dasycladus* which are isogamous. Indeed, these exceptions are so numerous as to constitute a serious obstacle to full acceptance of the synthetic theory, despite the general trend of the data. A detailed investigation of these apparently aberrant cases would be of great interest.

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REFERENCES

- BELK, D. (1977). *Southwest Nat.* **22**, 99.
 BLAXTER, J. H. S. & HEMPEL, G. (1963). *J. Cons. Perm. Int. expl. Mer.* **28**, 211.
 BOLD, H. C. (1973). *Morphology of Plants*, 3rd edn. New York: Harper & Row.
 CHARLESWORTH, B. (1978). *J. theor. Biol.* **73**, 347.
 DITTMER, H. J. (1964). *Phylogeny and Form in the Plant Kingdom*. Princeton, N.J.: Van Nostrand Publ. Co.
 DOGIEL, V. A. (1965). *General Protozoology*. Oxford: Clarendon.
 FINLEY, H. E. (1939). *J. exp. Zool.* **81**, 209.
 FISHER, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon.
 FRITSCH, F. E. (1935). *The Structure and Reproduction of the Algae*. 2 vols. Cambridge: Cambridge University Press.
 GHISELIN, M. T. (1974). *The Economy of Nature and the Evolution of Sex*. Berkeley, California: University of California Press.

- GRELL, K. G. (1967). In *Research in Protozoology* (T-T. Chen ed.). Vol. 2, pp. 147-214. Oxford: Pergamon.
- GRELL, K. G. (1973). *Protozoology*. New York: Springer.
- KALMUS, H. (1932). *Biol. Zentralblatt* **52**, 716.
- KALMUS, H. & SMITH, C. A. B. (1960). *Nature*, **186**, 1004.
- KERFOOT, W. C. (1974). *Ecology* **55**, 1259.
- KNOWLTON, N. (1974). *J. theor. Biol.* **46**, 283.
- LAWLER, L. R. (1976). *Evolution* **30**, 775.
- LEVINE, R. P. & EBERSOLD, W. T. (1960). *Ann Rev Micro.* **14**, 197.
- LEWIN, R. A. (1954). In *Sex in Microorganisms* (D. H. Wenrich, ed.), pp. 100-133. Washington D.C.: Am. Ass. Adv. Science.
- MARSHALL, J. A. (1953). *Evolution* **7**, 328.
- MAYNARD SMITH, J. (1978). *The Evolution of Sex and Recombination*. Cambridge: Cambridge University Press.
- PARKER, B. C. (1971). In *Contributions in Phycology* (B. C. Parker & R. M. Brown, eds), pp. 47-52. Privately published by The Students of Harold C. Bold.
- PARKER, G. A., BAKER, R. R. & SMITH, V. G. F. (1972). *J. theor. Biol.* **36**, 529.
- PATRICK, R. (1954). In *Sex in Microorganisms* (D. H. Wenrich, ed.). pp. 82-99. Washington D.C.: Am. Ass. Adv. Science.
- PICKETT-HEAPS, J. D. (1975). *Green Algae*. Sunderland, Mass: Sinauer Associates.
- SALTHER, S. N. (1969). *Am. mid. Nat.* **81**, 467.
- SALTHER, S. N. & DUELLMAN, W. E. (1973). In *Evolutionary Biology of the Anurans* (J. L. Vial, ed.), pp. 229-249. Columbia: University Missouri Press.
- SCAGEL, R. F., BANDONI, R. J., ROUSE, G. E., SCHOFIELD, W. B., STEIN, J. R. & TAYLOR, T. M. C. (1965). *An Evolutionary Survey of the Plant Kingdom*. Belmont, California: Wadsworth Publ. Co.
- SCOTT, W. B. & CROSSMAN, E. J. (1973). *Freshwater Fishes of Canada*. Fish Research Bd Canada Bull 184.
- SCUDO, F. M. (1967). *Evolution* **21**, 285.
- SLEIGH, M. A. (1973). *The Biology of Protozoa*. New York: American Elsevier Publ. Co.
- SMITH, G. M. (Ed.) (1951). *Manual of Phycology*. New York: Chronica Botanica Co.
- STEWART, K. D. & MATTOX, K. R. (1975). *Bot. Rev.* **41**, 105.
- TURNER, F. B. (1962). *Q. Rev. Biol.* **37**, 303.
- WARE, D. M. (1975). *J. Fish Res Bd Can.* **32**, 2503.
- WENRICH, D. H. (1954). In *Sex in Microorganisms* (S. H. Wenrich, ed.), pp. 134-265. Washington, D.C.: Am. Ass. Adv. Science.
- WIESE, L. (1976). In *The Genetics of Algae* (R. A. Lewin, ed.), pp. 174-197. Oxford: Blackwell Scientific Publ.
- WILLIAMS, G. C. (1975). *Sex and Evolution*. Princeton, N.J.: Princeton University Press.