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A Note on the Evolution of Gamete Dimorphism

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Parker, Baker & Smith (1972) have demonstrated mathematically that given the evolution of sexual reproduction, disruptive selection for the production of either many small gametes or a few large gametes may occur, resulting in a stable polymorphism of "sperm" and "egg" producers. Their model for the evolution of anisogamy requires only that zygote fitness (F) increase steeply with increases in zygote volume (V) (for $F \propto V^x$, x must be greater than 1·5) and that a sufficiently broad range of zygote productivity-size variants exist in the population (the higher the value of x, the broader the range needed). They suggest that anisogamy is almost universal in multicellular organisms but relatively rare in unicellular organisms because only for the former is an investment in extra gametic reserves at the expense of the number of gametes produced likely to be worthwhile in terms of increasing the survival probability of the zygote. In this note a graphical analysis and evidence from the anisogamous Protista will be presented concerning this hypothesis.

The hypothetical correlations of zygote fitness with zygote volume in multicellular and unicellular organisms are compared in Fig. 1. As Parker *et al.* point out, increasing the size of the zygote of a multicellular organism will in most cases significantly increase its fitness over a wide range of possible zygote sizes [Fig. 1(a)], because this will reduce the length of time the organism must spend in the risky developmental period or in other ways improve its chances of surviving until maturity. In a unicellular organism, however, the period of growth between fertilization and maturity is relatively insignificant; thus increasing the zygote size above a minimal threshold value will generally result in only small improvements in zygote fitness [Fig. 1(b)]. Comparing the two curves, one sees that the range of zygote volumes for which $1{\cdot}5 < x < \infty$ is much smaller for unicellular organisms, and the average value of x in this range is higher. Thus it is quite likely that for unicellular organisms the spread of zygote volumes where x takes on the appropriate values is below that required by the model for the action of disruptive selection.

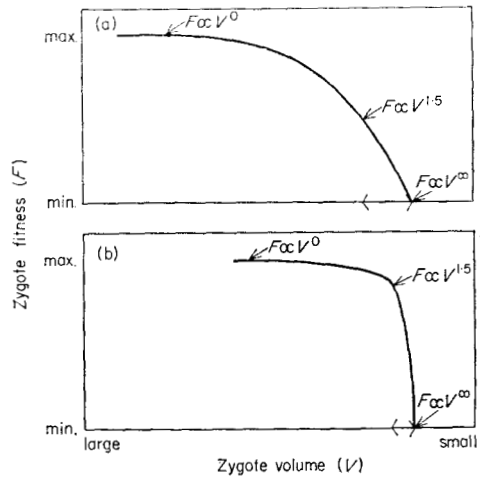

FIG. 1. The hypothetical relationship between zygote fitness (F) and zygote volume (V) in (a) multicellular and (b) unicellular organisms. The value of x ($F \propto V^x$) at any point along the curve is equal to the negative slope of the tangent to that point. The range of zygote volumes for which $1\cdot5 < x < \infty$ is indicated by carets along the abscissa. [Fig. 1 (a) after Parker *et al.*, 1972].

If this analysis is correct, then one would expect to find among the anisogamous Protista support for the hypothesis that as adult size is increased, zygote fitness becomes more strongly correlated with zygote size over a wider range of zygote sizes, leading to disruptive selection and the evolution of anisogamy. One group with potential for testing this hypothesis is the class Sporozoa; particularly in the orders Coccidia and Haemosporidia, distinct anisogamy with disassortative fusion is typical (Dogiel, 1965; Kudo, 1966). The size of the oocyst (the product of zygote development), however, is not particularly large in comparison to the size of the mature stages of other protists (Kudo, 1966). Thus if the zygote fitness-volume correlation is similar to that hypothesized for multicellular organisms, the reasons behind the similarity may not be the same. It is also possible that anisogamy in this case has evolved by a mechanism different from that proposed by Parker *et al.*, perhaps one related to the specialized parasitic life cycles, often involving intracellular stages, which are typical of these orders.

The only other protist group in which anisogamy can be considered common is the family Volvocidae (class Mastigophora, order Phytomonadida) (Dogiel, 1965; Kudo, 1966). If one arranges the genera of this family of colonial flagellates in order of increasing colony size (as indicated by the number of constituent cells) an interesting pattern emerges (Table 1). Genera

TABLE 1

The colony size and degree of gamete dimorphism in seven genera of the family Volvocidae

Genera	No. cells/colony	Gamete condition
Gonium	4 or 16	isogamy
Stephanosphaera	8 (4 or 16)	isogamy
Pandorina	16 (8 or 32)	slight anisogamy, no disassortative fusion
Eudorina	32 (16)	anisogamy, disassortative fusion
Platydorina	32	anisogamy, disassortative fusion
Pleodorina	32, 64 or 128	anisogamy, disassortative fusion
Volvox	180 – 15,000	anisogamy, disassortative fusion

Figures in parentheses under No. cells/colony indicate infrequent conditions. (Data from Dogiel, 1965; Kudo, 1966. Genera for which no information was available have not been included.)

with small colonies are isogamous, the genus with intermediate-sized colonies is barely anisogamous with no disassortative fusion, and genera with large colonies are distinctly anisogamous with definite disassortative fusion. This is exactly what one would predict from the Parker *et al.* hypothesis, and thus lends support to their model for the evolution of anisogamy.

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