

GENETIC POLYMORPHISM AS EVIDENCE OF OUTBREEDING IN GRAPTOLIDS

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ABSTRACT. Since graptoloids occupied a relatively stable and little differentiated pelagic biotope, numerous instances of genetic polymorphism within their species may be considered as indirect evidence of outbreeding as the mode of their reproduction. Under such conditions genetic polymorphism could be maintained mainly as a result of the heterotic effect, and outcrossing is the only way to provide the requisite heterozygosity.

THE mode of reproduction in the Graptoloidea is of crucial significance in understanding the mechanism of evolution in this group of extinct colonial animals. This is particularly true if one presumes a hermaphroditic nature of graptoloid zooids, as suggested by Kozłowski (1949). He attempted to explain elimination of the bithecae (which presumably housed the male zooids in the dendroid ancestors of Graptoloidea) and preservation of only one type of thecae (corresponding to autothecae which in the Dendroidea presumably housed the female zooids) by a shift from gonochorism to hermaphroditism.

If graptoloid zooids were hermaphroditic, two different modes of sexual reproduction were possible: (1) inbreeding (by means of self-fertilization or fertilization among members of the same colony) and (2) outbreeding (by means of cross-fertilization between members of different colonies). Each of these modes of reproduction will determine a different evolutionary 'strategy'.

Discrimination between these two modes of reproduction in graptoloids must obviously rely on indirect evidence only, such as the probable morphophysiological organization of graptoloid colonies and the patterns of their evolution.

Urbanek (1973) has analysed at some length the organization and presumed reproductive biology of graptoloid colonies. The colonies are collective units composed of a number of interconnected zooids, formed by budding from a single founder zooid, and, therefore, sharing the same genotype. The latter factor, combined with the presumed hermaphroditism of zooids, suggests the possibility of inbreeding as the mode of reproduction in the graptoloids because any fertilization among members of the same colony would result genetically in selfing. Urbanek also pointed out that protandry (earlier appearance of the male phase) would have been rather ineffective in ensuring cross-fertilization in graptoloid colonies because of differences in age among zooids within a single colony. For this reason male and female phases probably occurred contemporaneously among zooids of the same colony. He also excluded the possibility of a colonial control in spawning sperm and ova within the same colony at different times, because of lack of any traces of cyclic phenomena in the morphogenesis of graptoloids, such as those recognized in bryozoans.

On the other hand, Urbanek (1973) found that in the Graptoloidea major features of evolution are more in accordance with outbreeding than inbreeding as the mode of

reproduction. This is indicated by the existence of numerous bradytelic lines (persisting without change, while inbreeding would most likely imply either rapid change or extinction), and by a great morphological cohesion of widely spread (cosmopolitan) species, indicative of intense gene flow between panmictic populations. Urbanek suggested that incompatibility genes may have been the main factor responsible for outbreeding in graptoloids. However, the thesis that outbreeding has been the main mode of reproduction in Graptoloidea needed further evidence.

In our opinion such evidence can now be supplied by discontinuous intraspecific variation in graptoloids. Occurrence of what was considered as sharply delimited morphological phases (morphs) within a graptolite species was explained by Skevington (1966, 1967) as an instance of genetic polymorphism. There is now a growing body of data to support the view that genetic polymorphism was both widely spread among graptoloids and played an important role in the evolution of this group (Urbanek 1963, 1970; Jaanusson 1973). Recent considerations by Jaanusson (1973) also suggest that some 'megaevolutionary' events (such as the origin of uniserial monograptids from their biserial ancestors) were initiated by genetic polymorphism.

The thesis of the present contribution is that, in addition to the other evidence, occurrence of genetic polymorphism in graptoloids may be indicative of outbreeding. Genetic polymorphism *per se* has, of course, only indirect bearing on the breeding system of a given species because it has been recognized in both gonochoristic and hermaphroditic organisms (Ford 1964). However, there exist different processes which control the maintenance of genetic polymorphism and these processes are in part associated with differences in reproductive biology of the species.

Genetic polymorphism is maintained in a population by three processes. (1) Heterosis, that is, superior fitness of heterozygotes. (2) Diversifying ('disruptive') selection that favours the different genotypes in a strongly differentiated (mosaic) environment (Ford 1964; Svirezhev and Timoféeff-Ressovsky 1966; Timoféeff-Ressovsky and Svirezhev 1966; Mayr 1970; Dobzhansky 1970). (3) Random walk, that is, the polymorphism is maintained in a population by the balance between mutation and random drift (Kimura and Crow 1964; Wright 1966; Dobzhansky 1970). With regard to graptoloids the second process is not likely because the environment has probably been highly uniform (pelagic realm) although certain cyclic changes in the environment and seasonal selection cannot be entirely eliminated as responsible factors. Random walk operates when phenotypic characters are selectively neutral or nearly neutral. However, in graptoloid species the known polymorphic characters (for a summary, see Jaanusson 1973) have mostly a strong phenotypic effect and hence were scarcely neutral with respect to selection. Thus the superior fitness of heterozygotes seems to have been the most likely process for maintaining genetic polymorphism in the graptoloid populations which have lived in a relatively stable pelagic environment. The studies by Svirezhev and Timoféeff-Ressovsky (1966) and Timoféeff-Ressovsky and Svirezhev (1966) support this suggestion.

Since the heterotic effect can be produced operatively only as a result of outbreeding, which in each generation ensures the necessary supply of heterozygotes (Crow and Kimura 1965), this was probably the main breeding strategy of graptoloids. The opposite strategy, namely inbreeding due to selfing (fertilization among the zooids of the same colony sharing the same genotype), leads to an increase of homo-

zygosity, the homozygotes producing only homozygotes and half of the heterozygotes in each generation producing also homozygotes. In a relatively stable and little differentiated environment self-fertilization would ultimately lead to producing monomorphic populations in spite of selective superiority of heterotic polymorphs in natural selection. It should also be noted that among recent hermaphroditic animals self-fertilization seems to be rare since various mechanisms are known that reduce or completely eliminate this process.

The growing number of probable instances of genetic polymorphism in the graptoloids and the important role played by polymorphism in the mode of evolution of the group seems thus to be a strong argument in favour of outbreeding as the main mode of reproduction in graptoloids. This does not exclude the possibility of a rather flexible approach to the breeding strategy within Graptoloidea. In certain extreme conditions the mode of breeding may have changed into selfing, analogously with some recent hermaphroditic organisms (Ford 1964). Urbanek (1973) has even suggested that outbreeding, with a certain share of self-fertilization, may have provided graptoloids with a highly advantageous breeding system which may have been one of the reasons for their evolutionary success during the early Palaeozoic.

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