Reports

Oviparous Hermaphroditic Fish with Internal Self-Fertilization

Abstract. Adults of *Rivulus marmoratus* (Cyprinodontidae) contained eggs when dissected or laid eggs when kept alive. They invariably oviposited solo, emitting eggs in various developmental stages. Both juvenescent and senescent fish have functional ovotestes. Progeny (F_3) were obtained via a selfed great grandparent, grandparent, and parent, the last two in isolation *ab ovo.*

From morphological and related evidence it has been inferred that functional hermaphroditism is normal and widespread among serranids, sparids, and maenids (*1*), and perhaps some iniomous fishes will be added to this list (*2*). As recorded elsewhere, hermaphroditism in fishes is a sporadic, teratological phenomenon occurring in a variety of teleosts. The reproductive activities of normally hermaphroditic fish have not been described, except for the diminutive serranid *Serranellus subligarius* (Cope) (*3*).

The present report concerns observations made from 1958 to 1961 on a series of hermaphrodites of *Rivulus marmoratus* (Poey), a cyprinodontid of a tribe with chiefly Neotropical, Ethiopian, and Oriental forms, as compared to the more generalized and mostly North and Central American tribe of *Fundulus* and its allies (*4*). *Rivulus marmoratus*, a lately recognized component of the continental North American fauna (*5*), inhabits zones of alternate desiccation and tidal-pluvial flooding from Key West north at least to Vero Beach, Florida. It occurs also in Cuba and in the Bahamas and has a subspecies in the Antilles (*6*). Unlike many of its congeners, it prefers brackish waters but thrives in our fresh-water aquaria. In other species of *Rivulus* the caudal base ocellus differs between males and females. All specimens examined from the small extant collections of the superspecies have shown the presumptive female condition; all those dissected contained eggs, although both sexes are recorded for the subspecies (*6*). Our search for males led to the discovery of hermaphrodites among the presumed females.

Eight fish, seven directly from the wild and one in captivity since January 1958, have been closely observed and segregated from other fish since June 1960. All of them have oviposited. Despite indications of senescence, the oldest was producing fertile eggs after 32 months in captivity. Histological sections of its gonads disclosed actively functional ovotestes. Another, in isolation for over a year, now shows signs of aging but continues to emit eggs from which young hatch. An egg from this fish, oviposited after the fish had been in isolation 25 days, was incubated, and the hatchling was reared in isolation. After 6 months this hatchling began to lay eggs. One of its eggs, in turn, was isolated, and the hatchling from this egg began to oviposit within 4 months of eclosion. A sectioned fish comparable in size and age to the last-mentioned fish at first oviposition had ovotestes with developed eggs and with sperm ducts filled by spermatids and a few spermatozoa.

Daily observations have been made throughout the year on these and other individuals to record seasonal and diurnal periodicities in behavior, oviposition, back-calculated fertilization (ovulation?) times, and the durations of intra- and extraparental incubation. These findings and the histogenesis of the gonads cannot be described here except for salient features. The ovotestes exhibit territorial localization of the alternative gametogenic tissues. Eggs are oviposited at stages ranging from that in which the yolk vesicles and fertilization cone are disappearing to that in which the vitelline circulation is established—that is, from fertilization to Oppenheimer stage 22 (*7*).

Among hermaphrodites of *Rivulus marmoratus* that shared an aquarium, no obvious reproductive pairing was observed. The cyprinodont sigmoid, sexual flexure, and antecedent postures, as well as oviposition itself, were consistently assumed by single fish unattended by others. In *Serranellus subligarius*, on the other hand, cross-fertilization between hermaphrodites seems to be the rule and self-fertilization the exception, these fish alternating within minutes between the male and the female sexual role, changing their color pattern to suit the role (*3*). The former species is paludal and euryhaline; the latter, marine and stenohaline.

At the present writing, what appear to be three males with nuptial color have just developed from laboratory-produced eggs. These comprise a small proportion of the individuals examined, both from the wild and from our laboratory stock. If these three prove truly gonochoristic, the respective roles of hermaphrodites and gonochorists in the reproductive economy of the species come into question, and the possibility that sex determination is ecologically conditioned is being examined experimentally. In view of internal egg retention by the hermaphrodites for as long as over 2½ days of development, coition might be expected to produce mixed self- and male-fertilized eggs. The ovotestes have the gross appearance of ovaries and could only be distinguished from ovaries, if they exist, by laborious procedures; hence, the statistical incidence of putative female gonochorists would be difficult to determine.

Although the species is basically oviparous, *Rivulus marmoratus* shows a trend toward ovoviviparity—a disposition foreshadowed by an instance of egg retention by *Oryzias* (*8*), with phylogenetic implications because of the occurrence of oviparity, ovoviviparity, and viviparity within the order Cyprinodontiformes. This ambivalence may extend as well to hermaphroditism versus gonochorism, but the demonstrated frequency of hermaphroditism in this species affords unique access to prob-

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Instructions for preparing reports. Begin the report with an abstract of from 45 to 55 words. The abstract should *not* repeat phrases employed in the title. It should work with the title to give the reader a summary of the results presented in the report proper.

Type manuscripts double-spaced and submit one ribbon copy and one carbon copy.

Limit the report proper to the equivalent of 1200 words. This space includes that occupied by illustrative material as well as by the references and notes.

Limit illustrative material to *one* 2-column figure (that is, a figure whose width equals two columns of text) or to *one* 2-column table or to *two* 1-column illustrations, which may consist of two figures or two tables or one of each.

For further details see "Suggestions to contributors" [*Science* **125**, 16 (1957)].

lems of sexual physiology and the means of adding a highly homozygous strain of fish to the very few now available (*9*). To the latter end, it is planned to assess, by means of fin transplantation (*10*), the degree of genetic relationship among monoparental siblings and other progeny and parents of this species (*11*).

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Influence of Dead-End Pores on Relative Permeability of Porous Media

Abstract. The network model is used to show that wetting phase relative permeability of porous media is only slightly influenced by the fraction of that phase trapped in dead-end pores. On the other hand, the trapping of nonwetting phase in dead-end pores is a major influence on the shape of the nonwetting phase relative permeability curve. Laboratory experiments on porous media are suggested to test these network model predictions.

Simultaneous flow of two or more fluid phases occurs in soil, oil-bearing geological formations, and biological systems. In soils and biological systems the phases are water and air; in oil-bearing rock they are oil, water, and gas. Petroleum production technologists have made extensive studies of multiphase fluid flow in porous media and they have developed the definitions and working concepts.

For fluid systems of practical interest —water and air, or water, oil, and gas —there is usually only one fluid that wets the pore surfaces while the other (or others) do not. The wetting phase for water-air and for water-oil-gas is usually water. The wetting phase is believed to be spread over the pore surface; nonwetting phase occupies the center of the pore spaces and is surrounded by wetting phase.

When two or more fluid phases simultaneously occupy the pore space in a porous material the permeability to any phase is less than the single phase permeability. Permeability is defined as the volumetric rate of flow of a fluid of unit viscosity through a cube of unit cross section under a unit pressure gradient. The permeability of the porous material to any phase in the presence of other phases, divided by the single phase permeability, is known as the relative permeability. Relative permeability to a given phase is a function of the amount of that phase present in the pore spaces and is usually plotted as a function of "saturation," that is, the volume of a phase present divided by the total pore volume. Curves *A* and *E* of Fig. 1 are typical.

The factors that govern the shape of relative permeability curves are not yet well known. Studies of network models which point to the interconnection of pores into a network structure as the most important factor have been presented previously (*1, 2*). That there are other factors operating is indicated by the difference in shape of the wetting and nonwetting phase relative permeability curves.

In this paper, the previously reported network model data are reexamined to determine the amount of a given phase present in a network that is trapped in dead-end pores and therefore cannot flow. For single-phase flow, the network model has no dead-end pores and may be a good representation of real porous media, such as sandstone or sintered glass (*3*). When two immiscible phases are present in a porous medium, then the network model predicts that a situation may arise in which tubes (pores) filled with one phase cause some tubes containing the other phase to become dead-ends. There are no data on real porous media with which to check this prediction. Experiments on miscible displacement suggested at the conclusion of this report may give such data.

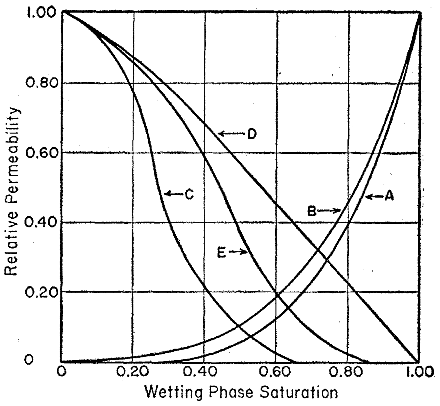

Fig. 1. Relative permeability curves for the network model (curves *A*, *B*, *C*, and *D*) and for sandstone (curve *E*). *A* and *C*, Wetting and nonwetting phase relative permeability, respectively, based on total volume; *B* and *D*, wetting and nonwetting phase relative permeability based on flowing volume; *E*, nonwetting phase relative permeability for sandstone.

The network data presented in this report, although of no quantitative significance when applied to real porous media, do indicate trends and the general appearance of relative permeability curves. These data can guide experiments designed to study the influence of pore structure on flow and diffusion in porous material.

The results of the reexamination of the data from an earlier paper (*1*, Figs. 5 and 6, pp. 147, 148; and Table 1, pp. 167, 168) are presented here as typical of networks which most closely represent real porous media (*4*).

At each saturation given in Table 1 of reference (*1*) the volume of each phase in dead-end tubes was recorded. This volume was subtracted from the total volume of the phase in the net-

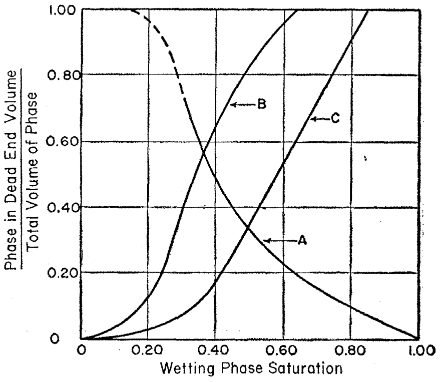

Fig. 2. Fraction of phase trapped in dead-end tubes. *A*, Wetting phase (from curves *A* and *B* of Fig. 1); *B*, nonwetting phase in network model (from curves *C* and *D* of Fig. 1); *C*, nonwetting phase for sandstone (from curves *E* and *D* of Fig. 1).