

leads to a reduction in density of the satellite DNA and probably to a relative enrichment of adenine and thymine. It may be conceived that the initial part of the molecule is particularly rich in these two compounds. Alternatively, one might think that the DNA polymerase, once detached from the template, continues to function in the synthesis of a polymer that contains mainly deoxyadenylate and deoxythymidylate (17).

If the first explanations were true, there should be, in theory, a decrease in the molecular weight of the cytoplasmic DNA. Nevertheless, this is not necessarily true because molecules especially rich in adenine and thymine can once again extend themselves by crossing-over: this is facilitated by the simple homologies that probably exist among the polymers very rich in adenine and thymine. The existence of crossing-over between different molecules of cytoplasmic DNA is, moreover, suggested by the work of Hudson and Vinograd (18). This existence is also indicated by the fact that (see Table 1) the cross between a ρ^+ and a ρ^- strain produces, in the absence of any treatment, new strains that have a satellite DNA density different from that of either of the parents.

The theory that we have set forth has the advantage of explaining the suppressiveness phenomenon. Mills *et al.* (9) have demonstrated that molecules from an RNA virus, replicating in vitro can be subjected to a selective pressure. If this selective force is simply the necessity to replicate quickly, it evolves, after a certain number of generations, into a new type of viral RNA that multiplies much more quickly than the initial one. The greater speed of replication is due to the fact that the new molecule is shorter and has a greater affinity for viral replicases. We think that exactly the same process operates in the DNA molecule mutated on the inside of the yeast cell. The incomplete DNA molecules produced by premature detachment of the DNA polymerase can multiply more rapidly than normal molecules, thereby leading to the phenomenon of pseudodominance, otherwise known as suppressiveness.

FRANCESCA CARNEVALI
Istituto di Fisiologia Generale,
Università, Rome, Italy

GIORGIO MORPURGO
Istituto Superiore di Sanità, Rome

GIORGIO TECCE
Istituto di Fisiologia Generale,
Università

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Two Unusual Unionid Hermaphrodites

Abstract. In a survey of the gonads of 97 species of North American freshwater mussels representing 59 genera, only four species were found to be hermaphroditic (monoecious). Among several other "occasional" hermaphrodites, two were unique in that the same follicles in the gonads produced eggs and sperm simultaneously. Evidently the control mechanism failed to function normally in these species [*Actinonaias ellipsiformis* and *Villosa* (formerly *Micromya*) *iris* (Lea)]. This simultaneous production of eggs and sperm is apparently quite unusual among mollusks.

In view of the rapid depletion of the mussel fauna, considerable effort has been made to collect and preserve properly relaxed and fixed specimens. Paraffin sections of 97 species, representing 59 genera, have been examined to determine to what extent these animals are monoecious or dioecious (1). The mussel fauna group is clearly dioecious (gonochoristic) with only four species (about 4 percent) found to be usually hermaphroditic (monoecious or ambisexual). Among the 1871 specimens sectioned, only one specimen each of two species, representing two genera, appeared abnormal, sperm and eggs being produced simultaneously in the same follicles.

While hermaphroditism is widespread among animals, the reasons for its development are poorly known. Several authors (2) have suggested that it may function in the survival of species living in habitats where the success of the reproductive process becomes difficult. Since most of the specimens collected in the same habitats and under similar conditions as the two featured here were normal, dioecious specimens, the theory that for these two specimens conditions were unfavorable seems unlikely. Although Purchon (3) concluded

that "in the majority of cases, hermaphroditism is an adaptive feature of evolutionary advantage to the species," he also indicated that there are perhaps stimuli other than environmental causes that account for this monoecious development. In addition to the strictly genetic factors, he indicated that the change may be initiated by the gonad itself since in the male phase there is a heavy consumption of nucleoproteins in the production of spermatozoa. The ratio between nucleoproteins and cytoplasm may be upset at a certain point so that sex-reversals are automatically affected. Whether genetic, hormonal, or cytogenetic, the reasons for the sex changes observed in freshwater mussels are, as yet, unknown.

Paraffin sections of 238 specimens of *Actinonaias ellipsiformis* (Conrad) have been studied. Males and females were clearly separable (108 females to 130 males). However, one specimen was an unusual hermaphrodite. Instead of having a predominance of male or female tissue and a small focus of tissue of the opposite sex (occasional hermaphrodites) as found in a number of other groups (1), tissues were extensively mixed so that it appeared that the mechanism of sex control was most

irregular (Fig. 1). Almost every possible combination from acini that are purely male or female to those that simultaneously produced sperm and ova within the same follicle occurred. The animal from which this tissue came was the oldest (estimated to be at least 10 years old) in the series of 12 males and 13 females. On the chance that senescence may have been a factor, the next largest specimen (measuring 67 mm and about 8 years old) was also examined; it was a normal male. The hermaphrodite evidently produced normal eggs since the posterior part of the outer gills still showed signs of having functioned as marsupia. This specimen, then, is a functional female hermaphrodite producing eggs and sperm simultaneously.

Although the predominantly female specimen of *Villosa* (formerly *Micromya*) *iris* (Lea) is not as extreme in the way the male and female phases are mixed within the gonad, the simultaneous production of both sex elements is, nevertheless, a prominent feature of its development.

Most of the eggs were developing normally (Fig. 1) and the gill structure of this specimen had the scars of spent marsupia from the previous spring. However, the walls of the acini as well as the contents of the same follicles show simultaneous spermatogenesis and oogenesis. The male aspects were not nearly as well developed as in *Actinonaias ellipsiformis*.

Coe (5) and Bacci (6) have classified the types of hermaphroditism in mol-

lusks. Apart from the two specimens discussed here, the number of mussels with hermaphroditic tendencies are relatively few. Apart from a number of mussels that are (1) "occasional" hermaphrodites, there were no members of the subfamily Unioninae among the usual hermaphrodites, there were three among the Anodontinae, and there was one in the large subfamily Lampsilinae. When the "reasons" are considered for the usual hermaphroditic species becoming monoecious, the possible explanations are far from clear.

In the case of *Anodonta imbecillis* the best series are taken in impounded waters above dams. It might be argued that the impoundment may represent an evanescent situation, but it does not explain why several other species that may occur with it did not develop hermaphrodites. However, the same type of habitat also seems to be the site in which another hermaphrodite, *Carunculina parva*, is usually found in abundance. There is now evidence that what appears to be the same, or a closely related species of *Anodonta imbecillis* in the south, is dioecious. *Lasmigona compressa* (and its eastern counterpart *Lasmigona subviridis*) is most abundant and best adapted to very small creeks far in the headwaters of drainages. During low-water stages such rivulets would be the first to dry, placing these animals in a very precarious situation. In such habitats *Lasmigona compressa* is often the only mussel to be found, and one might assume hermaphroditism is necessary for its survival. In this connection an effort is now being made to obtain properly preserved and fixed animals of *Uniomera tetralasmus*, which also occupies an inauspicious habitat in that it invades (as glochidia on fish) low-lying ground along rivers during flood periods. During the low-water stages, the mussels remain in aestivation in the ground.

HENRY VAN DER SCHALIE
 Museum of Zoology, Mollusk Division
 University of Michigan,
 Ann Arbor 48104

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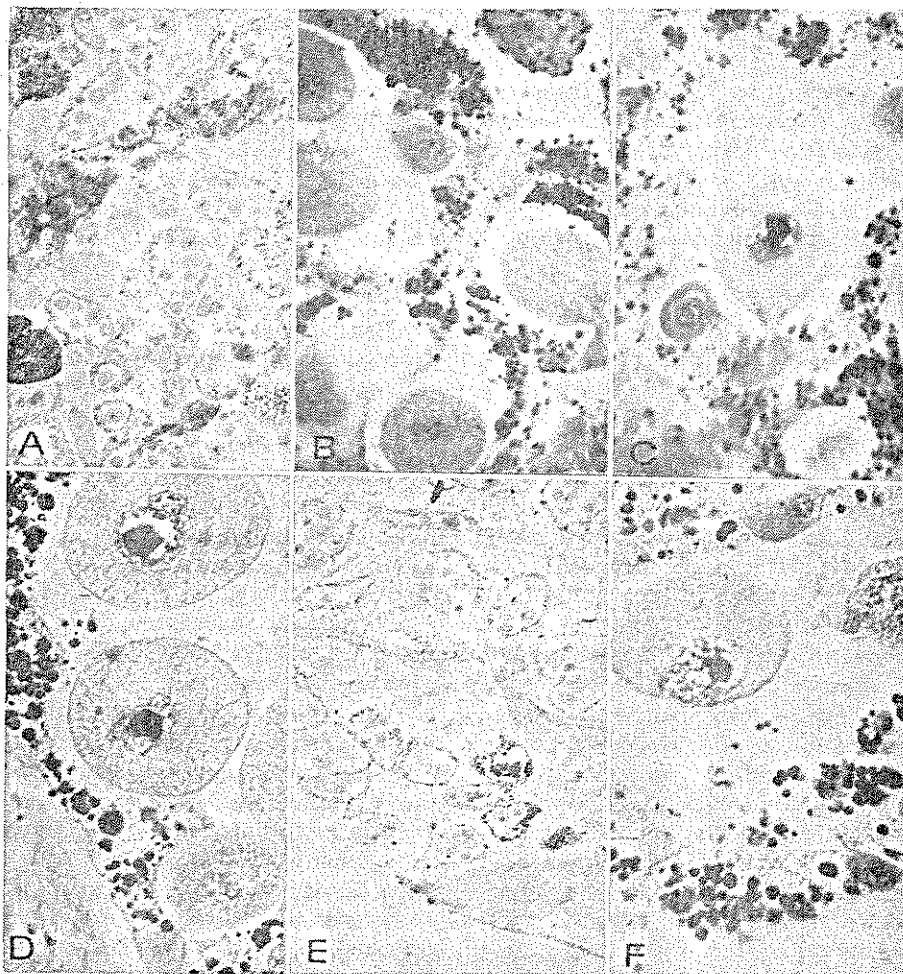


Fig. 1. Gonads of two species of freshwater mussels showing the simultaneous production of eggs and sperm in the same follicles. (A-D) *Actinonaias ellipsiformis* (Conrad); with (A) at low power ($\times 30$) and with (B), (C); and (D) at high power ($\times 120$) showing a view of three areas in the same gonad. Spermatogenesis is distributed in the walls whereas eggs are being produced from nurse cells; others of normal appearance occur in the lumen of the acinus. The same development is also shown in *Villosa* (formerly *Micromya*) *iris* (Lea) (E) and (F), with (E) taken at $\times 30$ magnification and (F) at $\times 120$. Both species were collected with a series in Michigan—*Actinonaias ellipsiformis* (Conrad) at Ore Creek below Hartland, Michigan, on 25 June 1959 (H. van der Schalie) and *Villosa iris* (Lea) at River Raisin, Sharon Hollow, Michigan, on 20 July 1962 (Norman Reigle).