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# The Genetics of the Mollusca

JAMES MURRAY

## Introduction

The available information on the genetics of the Mollusca is scattered in a rather disjointed fashion through the literature of malacology, ecology, marine biology, cytology, and even tropical medicine. The different facets of the subject have grown up independently of one another, each with its own internal logic. I have allowed these semiautonomous units to determine the organization of this review, retaining a historical coherence at the expense of a more systematic treatment. I trust that the following disparate subject headings will provide sufficient orientation for the reader.

## Reproduction

With something over 80,000 species, the phylum Mollusca encompasses a bewildering diversity of form and function. There is, of course, a basic body plan of "head-foot," soft visceral mass, and enveloping mantle, but the variations on this theme are protean, ranging from minute snails

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*TABLE 1. An Abbreviated Classification of the Molluscs, Indicating the Relative Position of Taxa Mentioned in the Text*[a]

| | |
|---|---|
| Class Monoplacophora | *Neopilina* |
| Class Amphineura (Chitons and solenogasters) | |
| Order Chitonida | |
| Class Gastropoda (Snails and slugs) | |
| Subclass Prosobranchia | |
| Order Archaeogastropoda | |
| Family Patellidae | *Patella* |
| Order Mesogastropoda | |
| Family Viviparidae | *Campeloma* |
| Valvatidae | *Valvata* |
| Littorinidae | *Littorina* |
| Hydrobiidae | *Potamopyrgus, Oncomelania* |
| Melaniidae | *Melanoides* |
| Calyptraeidae | *Calyptraea, Crepidula* |
| Order Neogastropoda | |
| Family Muricidae | *Purpura* |
| Subclass Opisthobranchia | |
| Order Cephalaspidea | |
| Family Actaeonidae | *Actaeonia* |
| Order Anaspidea | |
| Order Sacoglossa | |
| Order Notaspidea | |
| Subclass Nudibranchia | |
| Subclass Pulmonata | |
| Order Basommatophora | |
| Family Lymnaeidae | *Lymnaea* |
| Physidae | *Physa* |
| Planorbidae | *Planorbis, Biomphalaria, Bulinus* |
| Ancylidae | |
| Order Stylommatophora | |
| Family Succineidae | *Catinella* |
| Achatinellidae | *Achatinella* |
| Partulidae | *Partula* |
| Achatinidae | *Limicolaria, Rumina* |
| Arionidae | *Arion* |
| Philomycidae | *Philomycus* |
| Zonitidae | |
| Bulimulidae | *Liguus* |
| Helicidae | *Cochlicella, Monacha, Hygromia, Arianta, Cepaea, Helix* |
| Fructicicolidae | *Bradybaena* |
| Class Scaphopoda (Tusk shells) | |

*TABLE 1. Continued*

| | |
|---|---|
| Class Bivalvia or Pelecypoda (Clams, mussels, oysters and scallops) | |
| Order Taxodonta | |
| Family Arcidae | *Anadara* |
| Order Anisomyaria | |
| Family Mytilidae | *Mytilus, Modiolus* |
| Pectinidae | *Pecten* |
| Ostreidae | *Crassostrea* |
| Order Schizodonta | |
| Family Unionidae | *Unio* |
| Order Heterodonta | |
| Family Tridacnidae | *Tridacna* |
| Veneridae | *Mercenaria* |
| Order Adapedonta | |
| Family Myidae | *Mya* |
| Class Cephalopoda (Squids, cuttlefish, octopods and nautili) | |
| Order Octopoda | |

[a] Following Morton (1967), after Thiele (1931–1935).

to giant squids over fifty feet long. The abbreviated classification given in Table 1 will serve to introduce the forms discussed in this article.

Life histories and modes of reproduction in molluscs are as diverse as their body forms. Judging from primitive living forms, molluscan gonads originally opened directly into the pericardial cavity, and the eggs and sperms were swept into the sea through the coelomoducts. Fertilization was external, with the zygote developing first into a trochophore larva and then into a veliger adapted to a planktonic life. Sexes were probably separate.

From this primitive state, a number of trends may be discerned. Most groups of molluscs have developed some method of internal fertilization, and with this advance has come increasing complexity of the genital ducts and glands and the appearance of copulatory organs. In gastropods one can see a progression from forms (e.g., *Patella*) which shed their gametes directly into the water, via those (e.g., *Calyptraea*) with genital ducts consisting only of ciliated grooves in the mantle, to those (e.g., *Helix*) with fully enclosed systems, specialized stimulatory organs, and associated glands for processing eggs and spermatophores. Copulatory organs are of various types. Normally in gastropods a penis is developed from a portion of the foot, but in some forms (e.g., *Campeloma*) it is a modified tentacle. In *Actaeonia* the penis is armed with a spine so that

copulation takes place by hypodermic injection directly through the body wall. The cephalopods have perhaps the most bizarre form of sperm transfer, by means of a modified arm, or hectocotylus, which deposits spermatophores within the mantle cavity of the female.

Another trend in molluscs is toward the development of various methods of enhancing the survival of young. The eggs may be supplied with increasing amounts of yolk, and the free-swimming, vulnerable, larval stages may be reduced. Concomitantly, a tendency toward the brooding of eggs or young may develop. These changes are often associated with the colonization of more stringent habitats. In freshwater clams, for example, although fertilization is technically external (in the mantle cavity), the brood is maintained until hatching within the gill chamber. The larva (e.g., the glochidium of *Unio*) may be modified as a parasite of freshwater fishes. Freshwater and land gastropods suppress the larval stages altogether, in extreme cases retaining the eggs within the oviduct until hatching (e.g., *Partula*). Cephalopods also lay large, yolky eggs and care for them with elaborate brooding behavior.

Still another general trend, especially in gastropods, is toward either hermaphroditism or alternating sexuality. In amphineurans, scaphopods, cephalopods, and streptoneuran gastropods the sexes are separate, but the higher gastropods are increasingly committed to hermaphroditism, with (e.g., *Lymnaea*) or without (e.g., *Helix*) self-fertilization. The other method of relaxing the restrictions of sexuality is by means of consecutive or alternating sexuality. In the classic case of *Crepidula* each individual begins life as a male, then becomes a hermaphrodite, and later a female. Mating chains are arranged in stacks with females below and a young male at the summit. Other forms such as *Valvata* undergo rhythmic changes, with alternating episodes of male and female gametogenesis. Parallel developments are found in the pelecypods, *Mercenaria* undergoing protandric sex reversal and oysters showing alternating sexual states.

True parthenogenesis is rare in molluscs but has been convincingly demonstrated in the snails *Potamopyrgus, Campeloma,* and *Melanoides.*

For a highly readable introduction to molluscan biology, *Molluscs* by J. E. Morton (1967) may be recommended. Further details may be pursued in Volume V of *Traité de Zoologie,* edited by Grassé (1960 and 1968).

## Polymorphism in the Helicidae

The land snails of the family Helicidae exhibit extensive variation in color and in the ornamentation of the shell with longitudinal bands

(Taylor, 1914). The investigation of the genetic basis of this polymorphism had already commenced at the time of the rediscovery of Mendel's laws, and Lang's (1904) paper on *Cepaea hortensis* and *C. nemoralis* provides some of the earliest examples of Mendelian segregation in animals. The breeding of helicids was continued in the early decades of this century by Stelfox (1915, 1918, 1968), Oldham (1934), and Diver (Diver, 1932; Fisher and Diver, 1934). Although much of this work remains unpublished, Cook and King (Cook, 1965, 1967, 1969, 1970; Cook and King, 1966) have provided accounts of the results.

With the development of studies on the control of gene frequencies in natural populations of *Cepaea* (e.g., Cain and Sheppard, 1950, 1954; Lamotte, 1951, 1959; Clarke, 1960; Goodhart, 1962; Cain and Currey, 1963; Murray, 1964), the need for a better understanding of the genetics of land snails became apparent. Over the past 20 years a fairly clear picture of the genetics of *C. nemoralis* and *C. hortensis* has emerged. In addition, some data are available for *Arianta arbustorum, Helix aspersa, Cochlicella acuta, Monacha cantiana,* and *Hygromia striolata.*

## *Cepaea nemoralis*

Both in field studies on gene frequencies and in laboratory breeding *C. nemoralis* has received the greatest attention. It is a fairly large and colorful animal inhabiting much of western Europe and introduced into a number of places in the United States. The shell may be brown, pink, yellow, or white and may bear up to five (or rarely more) longitudinal stripes or bands. The various patterns of bands are conventionally indicated by number from the suture down to the umbilicus. Thus, 12345 represents the full five-banded condition, while 00345 indicates that the two uppermost bands are missing. A colon (as in 00:45) indicates the reduction of a band to an indistinct trace. The known genetic variations affect the color of the shell, the color of the dermal pigment, and the development, color, and modification of the bands. The loci and alleles determining these characters are summarized in Table 2.

The *C, B, I, S,* and *P* loci are associated in one tight linkage group. The resulting "supergene" provides a mechanism whereby natural selection can maintain the linkage disequilibrium often observed in natural populations, i.e., with coupling or repulsion chromosomes present in greater than expected proportions. There is some evidence that recombination frequencies may vary in different lines (Fisher and Diver, 1934; Lamotte, 1954; Cain *et al.,* 1960; Cook and King, 1966; Cook, 1969). The *U, T,* and *R* loci, although unlinked to the supergene, are

*TABLE 2. Loci and Alleles of C. nemoralis*

| | *Locus* | | *Alleles*[a] | | *References* |
|---|---|---|---|---|---|
| linked | *C* | Ground color of shell | $C^{B}$ | Brown | Lang (1904, 1908), Stelfox (1918), Lamotte (1951, 1954), Cain and Sheppard (1957), Cain *et al.* (1960, 1968) |
| | | | $C^{DP}$ | Dark pink | |
| | | | $C^{PP}$ | Pale pink | |
| | | | $C^{FP}$ | Faint pink | |
| | | | $C^{DY}$ | Dark yellow | |
| | | | $C^{PY}$ | Pale yellow | |
| | *B* | Presence or absence of bands | $B^{0}$ | Unbanded | Lang (1904, 1908), Darbishire (1905), Lamotte (1951, 1954), Cain and Sheppard (1957) |
| | | | $B^{B}$ | Banded | |
| | *I* | Punctate bands | $I^{I}$ | Punctate | Lang (1908, 1912), Stelfox (1918), Lamotte (1951), Cook (1967), Cain *et al.* (1968) |
| | | | $I^{-}$ | Unmodified | |
| | *S* | Spreading of band pigment | $S^{S}$ | Spread bands | Cain *et al.* (1960, 1968) |
| | | | $S^{-}$ | Unmodified | |
| | *P* | Pigmentation of bands and lip | $P^{N}$ | Normal (dark brown) bands and lip | Lang (1904, 1908, 1911), Stelfox (1918), Lamotte (1951), Murray (1963), Cook (1967), Cain *et al.* (1968) |
| | | | $P^{L}$ | Light brown bands and lip[b] | |
| | | | $P^{A}$ | White lip and normal bands (albolabiate)[b] | |
| | | | $P^{T}$ | White lip and transparent bands (hyalozonate) | |
| | *U* | Suppression of bands 1, 2, 4, and 5 | $U^{3}$ | Mid-banded (00300) | Lang (1912), Lamotte (1951, 1954), Cain and Sheppard (1957) |
| | | | $U^{-}$ | Unmodified | |
| | *T* | Suppression of bands 1 and 2 | $T^{345}$ | Bands 1 and 2 suppressed (00345) | Lamotte (1954), Cook (1967) |
| | | | $T^{-}$ | Unmodified | |
| | *D* | Dermal pigmentation | $D^{R}$ | Reddish dermal pigment | Murray (1963), Wolda (1969) |
| | | | $D^{G}$ | Gray dermal pigment | |
| | *Q* | Quantity of dermal pigment | $Q^{M}$ | Medium gray | Cain *et al.* (1968), Wolda (1969) |
| | | | $Q^{P}$ | Very pale (yellowish) | |

*TABLE 2. Continued*

| Locus | Alleles[a] | | References |
|---|---|---|---|
| *R* Darkening bands | $R^-$ | Unmodified | Cain *et al.* (1960), Cook (1969) |
| | $R^D$ | Bands gradually darken from apex to lip | |
| *O* Orange bands | $O^-$ | Unmodified | Cain *et al.* (1960, 1968) |
| | $O^O$ | Orange bands and lip | |

[a] Alleles are listed in order of decreasing dominance.
[b] The dominance relationships of $P^L$ and $P^A$ have not yet been established.

nevertheless associated with its expression, since $B^O$ is epistatic to *R*, *U*, and *T*, and $U^B$ is epistatic to *T*. Finally, $P^T$ is epistatic to some alleles at the *C* locus (Murray, 1963; Cain *et al.*, 1968).

A number of other segregating types are known, which may be assignable to these loci. Yellow-white, pale brown, and faint brown are probably determined by alleles at the *C* locus (Cain *et al.*, 1968). The 00:45 banding pattern is dominant to 00345 and may be an allele at the *T* locus (Cook, 1967). Yellow and red body color segregate, with yellow dominant, but it is not clear whether these types are controlled at the *D* locus (Wolda, 1969).

Still other conditions appear to be under multifactorial control. The width of bands varies such that at one extreme, banded shells may be indistinguishable from the phenotype determined by the $B^O$ allele (Cain *et al.*, 1968; Wolda, 1969); and at the other, extra, or satellite, bands may appear on phenotypes such as 00300 (Cook, 1967; Wolda, 1969). The fusion of adjacent bands (Cain *et al.*, 1960; Wolda, 1969) and shell size are also under polygenic control. Cook (1967) has estimated the heritability of size to be about 60 percent.

Variation in a number of enzymes and other proteins has been demonstrated by electrophoresis in *C. nemoralis* (Manwell and Baker, 1968; Levan and Fredga, 1972; Oxford, 1971, 1973*a*,*b*,*c*; Brussard and McCracken, 1974). By analogy with other organisms, it may be assumed that the variation is genetic, although the work of Oxford (1973*a*,*b*) has shown how difficult it is to draw direct conclusions in the absence of a thorough genetic and physiological study. He has shown three different patterns of inheritance for different groups of esterase bands. The first is a series of bands produced by a locus with five alleles. Since as many as five heavily staining bands may appear in a single individual, Oxford originally interpreted this as the expression of a compound locus resulting from a

*TABLE 3. Loci and Alleles of C. hortensis*

| | *Locus* | | *Alleles*[a] | | *References* |
|---|---|---|---|---|---|
| linked | *C* | Ground color of shell | $C^B$ | Brown | Lang (1904, 1908), Murray (1963), Cook and Murray (1966), Guerrucci (1971) |
| | | | $C^P$ | Pink | |
| | | | $C^{DY}$ | Dark yellow | |
| | | | $C^{PY}$ | Pale yellow | |
| | *B* | Presence or absence of bands | $B^0$ | Unbanded | Lang (1904, 1906, 1908), Murray (1963), Guerrucci (1971) |
| | | | $B^B$ | Banded | |
| | *P* | Pigmentation of bands | $P^N$ | Normal (dark brown) bands | Boettger (1950), Murray (1963), Cook and Murray (1966) |
| | | | $P^L$ | Light brown bands *(lurida)* | |
| | | | $P^T$ | Transparent bands (hyalozonate) | |
| | *I* | Punctate bands | $I^I$ | Punctate bands | Guerrucci (1971) |
| | | | $I^-$ | Unmodified | |

[a] Alleles are listed in order of decreasing dominance.

process of duplication. He has now shown, however, that phenocopies can be induced by changes in the diet of the snails, only two alleles being present in any one individual (G. S. Oxford, personal communication). The second pattern is the expression of a classic dimeric enzyme with three alleles at a single locus and triple-banded heterozygotes. The third pattern, originally thought to result from the presence or absence of activity at a single locus, has now been shown to display two active alleles, with no intermediate band in the heterozygote (G. S. Oxford, personal communication). Oxford (1973*c*) has emphasized that these enzymes in *Cepaea* are rather different in their physical and chemical properties from the esterases commonly found in vertebrates. Brussard and McCracken (1974) have also performed breeding experiments to show that two variable loci controlling leucine aminopeptidase (*LAP II*) and phosphoglucomutase (*PGM II*) display simple Mendelian inheritance, with three and two alleles, respectively.

The cytogenetics of *C. nemoralis* has recently been clarified by Bantock (1972), who has obtained unusually good preparations of chromosomes. There is a single very large pair, an intermediate pair, and twenty small pairs. Usually each chromosome shows only a single, localized chiasma, although the large pair may have up to four. Variation from population to population in the chiasma frequency in the large pair (Price, 1974) leads to the interesting speculation that this pair may

contain the elements of the supergene controlling the visible polymorphism.

## *Cepaea hortensis*

The principal interest in the polymorphism of *C. hortensis* is in the remarkable degree to which it parallels that of *C. nemoralis*. All the known loci of the visible polymorphism in the former (see Table 3) are found in the latter, and all show similar linkage relationships. In addition, homologies may be detected in two of the groups of polymorphic esterases (Oxford, 1973*b*). Indeed, it appears that these homologies extend to the other two species of the genus, *C. sylvatica* and *C. vindobonensis* (Oxford, 1971). An apparent exception was the orange-banded condition in *C. nemoralis* which is phenotypically similar to, but genotypically different from, the *lurida* form in *C. hortensis*. The predicted discovery of the $P^L$ allele in *C. nemoralis* restores the homology (Cook and Murray, 1966; Cook, 1967). Fusion of bands is multifactorially controlled in *C. hortensis* as in *C. nemoralis* (Lang, 1904; Murray, 1963).

*C. hortensis* and *C. nemoralis* can be crossed with great difficulty in the laboratory. Lang (1904, 1906, 1908) succeeded in producing some hybrids and showed that segregation and dominance were quite regular with respect to shell color, lip color, and banding pattern. The form of the love dart, the mucous glands, and the shape of the shell were intermediate. Manwell and Baker (1968) have interpreted similarities in the electrophoretic patterns of enzyme variation as evidence for hybridization in nature, but this aspect of the problem requires further study.

## *Arianta arbustorum*

The genetic system of *Arianta arbustorum* (see Table 4) shows some similarities to that of *Cepaea* (Cook and King, 1966). Two of the principal components are closely linked loci determining the color of the shell and the presence or absence of banding, although in the latter case the dominance is reversed and only a single, centrally placed band is developed. Other loci are less easy to relate. In general, *Arianta* is more cryptically colored than *Cepaea,* particularly as a result of the gene for mottling and of the reduced penetrance and expressivity of banding. The gene for transparent bands is probably not homologous with $P^T$ in *Cepaea*. There is a segregation for pale banding *versus* dark banding, which may be another allele at the *B* locus (Cook and King, 1966). An esterase polymorphism has been described by Levan and Fredga (1972).

*TABLE 4. Loci and Alleles of Arianta arbustorum*

| | Locus | | Alleles[a] | | References |
|---|---|---|---|---|---|
| linked | *C* | Ground color of shell | $C^D$ | Brown (dark pigment) | Oldham (1934), Cook and King (1966) |
| | | | $C^P$ | Yellow (pale, albino) | |
| | *B* | Presence or absence of a central band | $B^B$ | Banded | Cook and King (1966) |
| | | | $B^-$ | Unbanded | |
| | *F* | Mottling | $F^F$ | Mottled shell | Oldham (1934), Cook and King (1966) |
| | | | $F^-$ | Clear shell | |
| | *T* | Transparent band | $T^-$ | Nontransparent | Cook and King (1966) |
| | | | $T^T$ | Transparent band | |
| | *W* | White opaque stripe | $W^W$ | White opaque stripe | Cook and King (1966) |
| | | | $W^-$ | Unbanded | |

[a] Alleles are listed in order of decreasing dominance.

Components of shell size and shape are multifactorially controlled, with a heritability of about 60 percent (Cook, 1965).

## Other Species

*Helix aspersa* also displays a more restricted range of phenotypes than *Cepaea*. It shares with *Arianta* the crypsis resulting from heavy mottling. A suggestion of the color polymorphism of *Cepaea* remains, however, in the very young individuals, which may be either reddish brown or yellowish brown (Cain, 1971). Cain has shown that this difference depends on a single pair of alleles, with red dominant to yellow. At least one recessive gene (*exalbida* = albino shell and bands) affects both the color of the shell and the pigmentation of the bands (Stelfox, 1915, 1918; Cook, 1969). Cook suggests that by analogy with *Cepaea* this locus may represent two closely linked loci normally found in linkage disequilibrium in natural populations. Another segregation of a recessive, pale-banded condition may represent an additional allele at the *exalbida* locus. Two other loci control the reduction of the five-banded pattern (12345) to the formula 10005 and the delayed pigmentation of the bands *versus* normal pigmentation (Cook, 1969). By means of selection, Stelfox (1968) has shown that differences in shell shape are heritable. Enzyme polymorphisms have been described by Selander and Kaufman (1973*a*,*b*).

*Cochlicella acuta,* an elongate helicid, is polymorphic for at least three loci controlling the color and banding of the shell. Lewis (1968) has interpreted the banding as basically pentataeniate as in *Cepaea.* He has shown that the unbanded condition is recessive to 00040 and to the five-banded with all bands fused [indicated as (12345)]. 00040 is recessive to 00340, to (123)(45), and to (12345). It seems likely that these forms represent an allelic series, although the breeding results are not yet conclusive. Discontinuously opaque ostracum (DO) is dominant to continuously opaque ostracum (CO), and amber shell color segregates with colorless shell. Taken together with studies of chromosome frequencies in natural populations, the breeding experiments establish that the loci controlling the principal elements of the polymorphism, i.e., shell color, condition of the ostracum, and type of banding, are tightly linked and function as a supergene (Lewis, 1968).

In both *Monacha cantiana* (Cain, 1971) and *Hygromia striolata* (Cain, 1959*a,b*) there is segregation for dark and light coloration of the mantle. Cain has suggested in *Monacha* that dark is dominant to light and has shown that mantle color is independent of body color and shell color. Mantle and body color are correlated in *Hygromia,* although the color of the shell is independent.

## Asymmetry in Gastropods

Snails, which typically display asymmetrical coiling of the shell and viscera, may be classed as either dextral or sinistral. If the shell is held with the apex upward and the aperture facing the observer, a dextral shell will have the aperture on the right and a sinistral shell will have it on the left. Most species of snails are dextral, but many species and even whole genera (e.g., *Physa*) are sinistral.

It is not uncommon for species that are regularly dextral to produce occasional sinistral individuals and *vice versa.* More rarely, some species are truly amphidromic, producing both dextrals and sinistrals in the same population (e.g., *Partula suturalis*). Usually snails of opposite coil show true mirror-image reversal of the internal organs, but in some cases the shell may be dextral and the soft parts sinistral (e.g., *Planorbis*).

The genetics of coiling was first worked out by Diver and his colleagues in *Lymnaea peregra* (Boycott and Diver, 1923; Diver *et al.,* 1925; Boycott *et al.,* 1930; Diver and Andersson-Kottö, 1938). *L. peregra* is normally dextral, with some populations containing a small proportion of sinistrals. Diver and his co-workers showed that there is a major locus controlling the direction of coiling, with the allele for dextrality (*R*)

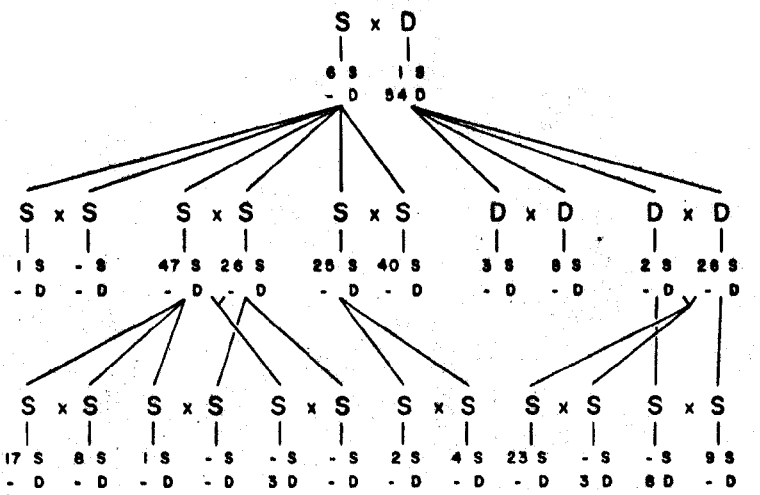


*Figure 1. The inheritance of the direction of coiling of the shell in Partula suturalis. S and D indicate the phenotypes of sinistral and dextral individuals. Lines indicate the parentage of individuals used for breeding. In three cases in the third generation, individuals used as parents were born prior to the separation of their parents and, therefore, can only be assigned to the pair. A fork at the origin of the line indicating parentage expresses this uncertainty.*

dominant to that for sinistrality (*r*). The trait shows a delayed Mendelian segregation, since the phenotype of a snail is determined by the genotype of the maternal parent. Thus, the genetic constitutions of the parents are displayed in the $F_1$, dominance is indicated by the phenotypes in the $F_2$, and segregation occurs by whole broods in the $F_3$ (Sturtevant, 1923).

In *L. peregra* a number of other genes are capable of modifying the sinistral (*r r*) type so that mixed broods of sinistral and dextral young are produced. Both sinistral and dextral types continue to produce mixed broods of similar compositions. Pure lines may be extracted, giving different proportions of modified young, high proportions being associated with lowered viability. Dextral lineages also produce sporadic sinistrals, but these seem to be genetically sinistral (Diver and Andersson-Kottö, 1938). The inheritance of one other character in *L. peregra* has been studied by Boycott and Diver (1927); albino body is inherited as a simple Mendelian recessive. Similar results have been obtained with coiling and color in another species of "*Limnaea*" from Hawaii by Crampton (1932*b*), although the data have not been published.

The inheritance of coiling in *Partula suturalis* is similar but more regular (Murray and Clarke, 1966, 1969). Since self-fertilization is less

common and crosses of dextral and sinistral individuals are more easily obtained, direct analysis of delayed segregation is facilitated. Figure 1 shows a typical lineage involving a cross between homozygous dextral and sinistral animals. The dominance of sinistrality is seen in the $F_2$ and segregation in $F_3$. Usually all offspring of any individual show one type of coil, but sporadic individuals of opposite coil are produced.

Among the Helicidae there seems to be no good evidence for the genetic determination of the rare cases of sinistrality. Bantock *et al.* (1973) record a mating of two sinistral individuals of *C. hortensis* which produced all dextral offspring (64), but in view of the delayed segregation expected in this case the observation is inconclusive. Bantock *et al.*, however, cite a report by Jeffries (1860) of a 100-percent sinistral race of *Helix aspersa.*

## Polymorphism in Other Gastropods

A number of other examples of genetic polymorphism have been investigated in gastropods. The available data vary from anecdotal accounts to reasonably systematic studies.

Because of the difficulty of rearing forms with pelagic larvae, very little work has been done on marine gastropods. Struhsaker (1968) has made a beginning with *Littorina picta.* She has managed to rear larvae derived from smooth and sculptured forms of this species. The extreme forms produce all smooth and all sculptured offspring, respectively, while intermediates produce very variable young. The inference is, therefore, that shell form is multifactorially determined. *Littorina mariae* and *L. obtusata,* which have no pelagic larvae, have recently been successfully bred by Reimchen (1974). He has shown that in *L. mariae* the two principal color morphs, reticulata and citrina, segregate in crosses. The most likely interpretation of the data is that two loci are involved with reticulata determined by the joint occurrence of dominant alleles at both. In *L. obtusata* he has shown segregation of three forms, reticulata, olivacea, and citrina. In *Purpura* (= *Thais*) *lamellosa,* Spight (1972) has shown that the patterns of shell color and banding are genetically controlled.

The remaining studies embrace forms from a number of different families of the Stylommatophora: Partulidae, Achatinidae, Bulimulidae, Philomycidae, Arionidae, and Fructicicolidae.

Two species of *Partula* have been bred by Murray and Clarke (1966, and unpublished). In *P. taeniata,* several shell colors show Mendelian segregation. Brownish purple, light brown, yellow, and white form an allelic series, with dominance descending in that order. Dominance is in-

complete in that homozygotes of the alleles for the darker colors are darker than heterozygotes with yellow or white. Pink shell is also dominant to yellow and white but is probably at a different locus. The reflected lip of the shell is usually white, but a single, dominant gene alters the color to pink. Another dominant converts the extreme apex of the shell to dark purple. Three types of banding patterns (frenata, zonata, and lyra, in the terminology of Crampton, 1932*a*) segregate with the unbanded condition. All are dominant to unbanded and segregate among themselves. The lyra pattern may also be formed by the joint presence of zonata and frenata in the same animal, suggesting that the lyra "allele" is composed of coupled dominants at the two closely linked loci. Indeed, shell color, lip color, spire color, and banding pattern are all so closely linked as to constitute a supergene.

In *P. suturalis,* Murray and Clarke (1966) have shown segregation for Crampton's (1932*a*) patterns, frenata, bisecta, atra, cestata, strigata, and apex. The indications are that all these patterns are under the control of a single, complex locus or supergene. In some populations, *P. suturalis* is amphidromic (for the genetics of coiling, see above). In both species of *Partula,* components of shell size show high heritability (Murray and Clarke, 1968).

From among the Achatinidae, Barker (1968) has investigated two species of *Limicolaria.* In both *L. flammulata* and *L. aurora,* streaked (*U*) is dominant to unstreaked (*u*) shell, and gray (*g*) is recessive to pink ($G^P$) in *L. aurora* and to brown ($G^B$) in *L. flammulata.* The *U* and *G* loci are tightly linked with deficiencies of the coupling chromosomes noted by Barker (1968). There may be another locus affecting the depth of pigmentation of the streaks. Owen (1969) has noted a similar polymorphism in *L. martensiana.* In another achatinid, Selander and Kaufman (1973*b*) have described genetic variation in a number of enzymes. Among European and North African populations, 16 of 25 enzyme loci are variable in *Rumina decollata.* Populations of this species introduced into North America are, however, apparently invariant at all of these loci from South Carolina to California.

The extravagant polymorphism in the bulimulid *Liguus fasciatus* has aroused great interest among shell collectors, but very little is known of the genetics of this species. Pilsbry (1912, 1946) recorded a single brood of eight offspring showing segregation for pink *versus* white spire (4 : 4) and unbanded *versus* banded (6 : 2). Presumably the difficulty in rearing these snails has deterred further work.

Ikeda (1937) has used the genetics of *Philomycus bilineatus* to show that uniparental reproduction in this species is by self-fertilization and not

parthenogenesis. Individuals heterozygous for a dominant gene producing three longitudinal black stripes on the mantle give rise to true-breeding striped (*A A*), heterozygous striped (*A a*), and true-breeding unstriped (*a a*) offspring in Mendelian proportions.

Two species of the Arionidae have been investigated. Abeloos (1944, 1945) has described a color polymorphism in *Arion hortensis* depending on three alleles at a single locus. The normal gray-blue ($C^B$) is dominant to pink ($C^r$), which is in turn dominant to white ($C^O$). The genetics of color in *A. ater* is more complex. Williamson (1959) has identified three loci controlling the type of pigment and its location. One determines the kind of melanin, with black (*M*) dominant to brown (*m*). A second locus affects the development of lateral longitudinal bands, the presence of bands (*U*) being dominant to their absence (*u*). A third locus, with three alleles, determines the extent of the dorsal pigmentation. Full color (*F*) is dominant to streaked ($f^s$), which is dominant to white (*f*). The white condition is epistatic to the *U* locus since pigment is found only in the tentacles or foot fringe. In addition, full-color individuals can only be scored for banding as juveniles since in adults the pigment spreads uniformly over the whole animal. The *F* and *U* loci are very tightly linked; no crossovers occurred in 474 offspring. The *M* locus segregates independently.

Finally, the polymorphism of *Bradybaena similaris* has been studied by Komai and Emura (1955). There are two principal loci: brown ($C^B$) is dominant to yellow (*C*), and banded ($S^t$) is dominant to unbanded (*S*). The two loci are closely linked, so closely that absolute linkage disequilibrium is possible. The $C^B S^t$ chromosome has not been found.

Thus, one can observe certain regularities in the polymorphisms of land snails. In general, there is at least one locus with several alleles for different colors, and there is another locus controlling the presence or absence of stripes or bands. These loci are usually tightly linked to form supergenes capable of maintaining linkage disequilibrium. It seems that the better known the genetics of any gastropod becomes, the more complex the supergene polymorphism is found to be.

## Genetics of the Pelecypoda

The economic importance of certain species of oysters and clams has stimulated a beginning on genetic studies of bivalves, despite the formidable technical problems involved (Chanley, 1961; Imai and Sakai, 1961, Longwell and Stiles, 1970; Menzel, 1972). Most of the work has

combined cytogenetics (for references, see below) and the methods of quantitative genetics.

The American oyster, *Crassostrea virginica,* shows all the characteristics of a highly outbred species (Longwell and Stiles, 1970, 1973). Full-sib crosses fail completely, with reduced fertilization (40 percent *vs.* 87 percent in controls), abnormal cleavage (97 percent *vs.* 30 percent in controls), and no larval setting. Polyspermy and parthenogenesis are increased. Since gamma irradiation reduces these effects, Longwell and Stiles (1973) suggest the existence of a system of incompatibility alleles similar to that found in many plants. The Pacific oyster, *C. gigas,* is less sensitive to inbreeding, as Imai and Sakai (1961) have been able to rear sib-mated lines for three generations.

Estimates of heritability of larval growth rates in *C. virginica* and *C. gigas* vary widely (Lannan, 1972; Longwell and Stiles, 1973) but suggest that these species possess sufficient additive genetic variance for commercial improvement by selection. On the other hand, Longwell and Stiles (1970) have detected nonadditive effects which should favor the development of hybrid commercial stocks. Parental stocks for producing hybrids would probably be obtained by intraspecific selection since most species crosses result in a high degree of developmental abnormality (Davis, 1950; Imai and Sakai, 1961). In contrast with these studies, however, Menzel (1968*b*, 1973) has reported normal development in crosses of several species of *Crassostrea* and normal meiosis in hybrids of *C. virginica* and *C. gigas* reared to adulthood. Interspecific hybrids between the clams *Mercenaria mercenaria* and *M. campechiensis* combine the desirable qualities of both species (Chestnut *et al.,* 1957; Haven and Andrews, 1957; Menzel, 1972), if indeed they are good species (Haven and Andrews, 1957; Menzel, 1968*b*).

The genetics of shell marking in *M. mercenaria* has been studied by Chanley (1961), who reared both $F_2$ and backcross progenies to show that white and brown clams differ at a single locus. The so-called *notata* "subspecies," with reddish brown zigzag lines, is the heterozygote. Chanley also showed, by means of selection experiments, that genetic variation in growth rate is quite marked in *Mercenaria.*

Genetic variation in the electrophoretic mobility of enzymes and other proteins has been described for a number of species of clams. Milkman and Beaty (1970) surveyed populations of *Mytilus edulis* and *Modiolus demissus* and detected three allozymes of leucine aminopeptidase (Lap) in each species. Different populations differed in gene frequencies, as did young and adults from single populations. Koehn and Mitton (1972) have shown that, although the Lap allozymes are different

in the two species, they nevertheless vary in a parallel fashion from population to population. *Mercenaria mercenaria* and *Pecten irradians* also have a three-allele Lap system, while *Mya arenaria* has two Lap loci with three alleles each. Malate dehydrogenase (Mdh) is also polymorphic in *Mytilus* and *Modiolus* (Koehn and Mitton, 1972); and "tetrazolium" oxidase, in *Modiolus* (Koehn *et al.*, 1973). Mitton and Koehn (1973) have investigated the relationship between Lap and aminopeptidase (Ap) in *Mytilus edulis*. They have found consistent nonrandom associations of the various alleles, with changes in the degree of association with increasing age.

Gooch and Schopf (1972), Levinton (1973), and Ayala *et al.* (1973) have surveyed enzymes in bivalves to assess the effect of environmental variability on genetic variability. These studies have detected a wealth of genetic variation (e.g., 25 polymorphic loci out of 30 surveyed in *Tridacna maxima* by Ayala *et al.*), but the relation between the two does not appear to be a simple one.

Schaal and Anderson (1974) have begun an electrophoretic study of variation in the American oyster, *Crassostrea virginica*. They have reported 13 polymorphic loci out of a total of 31 coding for 25 enzyme systems.

One of the two hemoglobins in the arcid clam *Anadara trapezia* occurs in two allelic forms (Nicol and O'Gower, 1967). A cline in gene f quency is correlated with the effects of currents on the east co tralia (O'Gower and Nicol, 1968).

## Cytogenetics

Reports of chromosome counts fo be found in the literature, dating t Many of the older accounts [fo however, of doubtful accuracy modern squash techniques. T molluscan cytogenetics has b work incorporates and ex (1938), Burch (1960*a*, Menzel (1968*a*).

Chromosome n molluscan classes. for one species of for two species of among the Gastr phopoda. Only th

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*TABLE 5. Chromosome Numbers Known for the Orders of Molluscs*

| *Group* | *Haploid number* | *References*[a] |
|---|---|---|
| Class Amphineura | | |
| Order Chitonida | 6 | Dolph and Humphrey (1970) |
| Class Gastropoda | | |
| Subclass Prosobranchia | | |
| Order Archaeogastropoda | 9–21 | |
| Order Mesogastropoda | 7–60[b] | |
| Order Neogastropoda | 13–36 | |
| Subclass Opisthobranchia | | |
| Order Cephalaspidea | 17–18 | |
| Order Anaspidea | 17 | |
| Order Sacoglossa | 7–17 | |
| Order Notaspidea | 12 | |
| Order Nudibranchia | 13 | |
| Subclass Pulmonata | | |
| Order Basommatophora | 15–72[b] | |
| Order Stylommatophora | 5–44 | |
| Class Bivalvia (Pelecypoda) | | |
| Order Anisomyaria | 10–14 | Ahmed and Sparks (1970) |
| Order Heterodonta | 12–23 | |
| Order Adapedonta | 17 | |
| Cephalopoda | | |
| Octopoda | 28 | |

[a]ditions as indicated.
[b]o be polyploid.

are well enough known to warrant a
ree of conservatism. For example,
16 different families, all have a
). With only a few exceptions,
have taken place by means of
(Husted and Burch, 1946;
2 bivalents from the basic

extensive hermaph-
ott, 1919; Rhein,
1965), polyploidy
ndividuals (Nata-
detected in four
anderson, 1940),
; Burch, 1967*a*),

and in two different subfamilies of the Planorbidae (Burch, 1960*c,d*, 1965, 1967*a,b*) including the medically important *Bulinus* discussed below. In every case polyploidy is expressed at the lower taxonomic levels and does not appear to have contributed to the evolution of higher categories.

Burch (1965) has remarked on the general tendency among the gastropods for the more specialized (evolutionarily advanced?) species to have higher chromosome numbers. This regularity argues against the popular theory that freshwater pulmonates (Basommatophora), which have a modal number $n = 18$, are derived from land pulmonates (Stylommatophora), which tend to have higher numbers. There are some notable exceptions, however, since *Catinella rotundata* among the Succineidae has the lowest number ($n = 5$) recorded for any mollusc (Burch, 1964).

The interpretation of chromosome numbers as an indicator of evolutionary status must be viewed with caution. Burch (1965) has pointed out that *Achatinella*, considered by Pilsbry (1900) to be among the most primitive of the Stylommatophora, also has the low chromosome number of $n = 20$. On the other hand, *Partula*, placed in an equivalent position by Pilsbry, has $n = 29$ (Scvortzoff, 1966), higher than most of the supposedly advanced Helicidae. Butot and Kiauta (Butot and Kiauta, 1969; Kiauta and Butot, 1969) have also suggested that there have been evolutionary trends toward lower numbers in the Helicidae and the Zonitidae.

When cytological details can be discerned, the chromosomes of molluscs are seen to be elongate with median, submedian, or terminal centromeres (Burch, 1960*a*). There has been disagreement over the occurrence and extent of chromosomal sex determination in molluscs with separate sexes (Jacob, 1959*b*; Nishikawa, 1962). Nevertheless, XY or XO mechanisms have been described for species from the Hydrobiidae (Burch, 1960*b*; Patterson, 1963), the Viviparidae (Patterson, 1965), and the Melaniidae (Jacob, 1959*a,b*). The sex chromosomes may be heterochromatic (Jacob, 1959*b*).

Supernumerary chromosomes have been noted in a number of species [see Patterson (1969) for references]. Evans (1960) has described a particularly notable example in *Helix pomatia* in which up to six additional chromosomes are present. They are smaller than the normal chromosomes but behave regularly during meiosis.

Finally, a most unusual example of intraspecific variation in chromosome number has been described in *Purpura* (= *Thais*) *lapillus* by Staiger (1954, 1955). On the coast of Brittany this muricid snail is represented by two "races," with $n = 13$ and $n = 18$. The 13-chromosome race has 8 acrocentrics and 5 metacentrics, whereas the 18-chromosome race has only acrocentrics. Studies of pairing in intermediate populations

show that each of the metacentrics is represented by 2 acrocentrics in the other race. About 1 percent of the animals are heterozygous for translocations, usually involving the metacentrics, so that multivalents are formed at meiosis. The differences in chromosome structure are correlated with the habitats of the populations. The 13-chromosome race inhabits rocky coasts with heavy surf while the 18-chromosome race is found in sheltered bays. Only the 13-chromosome race has been reported in North America.

## Genetics of Vectors of Schistosomiasis

The most pressing practical problems in molluscan genetics are to be found in the study of the vectors of schistosomiasis. The solution of the grave public health problems posed by this group of diseases may perhaps be found in the understanding and manipulation of the genetics of the vector species. These are *Biomphalaria* (= *Australorbis*) *glabrata* for *Schistosoma mansoni*, *Bulinus* spp. for *Schistosoma haematobium*, and *Oncomelania hupensis* ssp. for *Schistosoma japonicum*. *Biomphalaria* and *Bulinus* belong to the family Planorbidae while *Oncomelania* is in the Hydrobiidae.

A number of genetic markers are available for the study of *Biomphalaria glabrata*. The recessive gene for albinism (*c*) characterized by Newton (1954) has been used to demonstrate the precedence of cross-fertilization over self-fertilization (Newton, 1953; Paraense, 1955), to test for reproductive isolation between putative species (Paraense and Deslandes, 1955; Barbosa *et al.*, 1956), to test the genetic compatibility of allopatric populations within species (Paraense, 1956, 1959; Richards, 1962), and to investigate susceptibility to *Schistosoma mansoni* (Newton, 1955; Richards, 1970). Richards (1967) has described another allele at this locus, blackeye ($c^b$), which has dark eyes but no collar or body pigment and which may be used in crosses ($C\,c \times c^b\,c$) to determine that reciprocal cross-fertilization has occurred. Pearl formation, antler tentacles, and everted preputium (with swollen tentacles) are inherited as simple recessives (Richards, 1970, 1972, 1973*c*).

By means of selection and transfer from strain to strain, a number of other characters in *Biomphalaria* have been shown to be inherited, although most are variable in penetrance and expressivity. They include presence of "apertural lamellae" associated with a tendency to aestivation (Richards, 1968), tentacle and eye malformations (Richards, 1969*a*), mantle pigmentation (Richards, 1969*b*), and pulmonary occlusion, head bulb, scalariform shell, polyembryony, and hemolymph pigmentation (Richards, 1970, 1971). Mantle pigmentation may be selected in strains to

the point where it will segregate for at least one generation, with spotted dominant to unspotted. Head bulb and scalariform shell are sublethal.

The series of body-color alleles at the *C* locus in *B. glabrata* is also found in *B. straminea*. The latter species may be selected for mantle spotting as well, even the albinos sometimes showing this trait, a condition not found so far in *B. glabrata* (Richards, 1973*b*).

The susceptibility of *B. glabrata* to *S. mansoni* infection varies with age and strain. Juvenile susceptibility is multifactorially controlled (Newton, 1953; Richards, 1970; Richards and Merritt, 1972). Snails which are susceptible as juveniles may be either susceptible or resistant as adults, depending on a single locus, with resistance being dominant (Richards, 1970, 1973*a*).

Similar work has been begun by Davis and Ruff (1973) with *Oncomelania hupensis*. In crosses between geographical subspecies, body pigmentation and shell ornamentation are determined by two unlinked loci, with pigmented body dominant to albino and ribbed shell dominant to smooth. Susceptibility to *S. japonicum* seems to be multifactorially controlled [Davis and Ruff (1973); but see Chi *et al.* (1971)].

In *Bulinus*, the problem of susceptibility to *S. haematobium* is complicated by the confused and difficult taxonomy of the group. Many of the species are virtually impossible to identify by means of gross morphology. Burch (Burch, 1960*d*, 1967*b*; Burch and Lindsay, 1970) has begun to unravel the tangle by showing that populations with similar morphological characters may have different chromosome numbers, forming a polyploid series ($2n = 36$, $4n = 72$, $6n = 108$, $8n = 144$). Diploid species (*tropicus* species group) are resistant to infection, although in at least one instance an experimental infection has been achieved (Lo *et al.*, 1970). On the other hand, tetraploids (*truncatus* species group) are regularly susceptible, as is an octoploid species from Ethiopia (Lo, 1972). At least one genetic marker, a simple recessive gene for albinism, has been employed to follow the results of crosses between species (Wu, 1972, 1973).

A number of studies of the electrophoretic variation in the vectors of schistosomiasis have been undertaken (Wright *et al.*, 1966; Coles, 1969; Malek and File, 1971; Wium-Andersen, 1973), but the goal has usually been the identification of species in these difficult groups. Consequently genetic variation within species has generally been regarded only as a nuisance. Much more could be made of these characters as markers in genetic studies of these organisms.

The pioneering work that has been begun in the search for genetic answers to the problem of controlling schistosomiasis is being followed up actively in a number of laboratories around the world at the present time.

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