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# HANDBOOK OF GENETICS

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Volume 3  
Invertebrates of  
Genetic Interest

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# Preface

The purpose of the first four volumes of the *Handbook of Genetics* is to bring together collections of relatively short, authoritative essays or annotated compilations of data on topics of significance to geneticists. Many of the essays will deal with various aspects of the biology of certain species or species groups selected because they are favorite subjects for genetic investigation in nature or the laboratory. Often there will be an encyclopedic amount of information available on such species, with new papers appearing daily. Most of these will be written for specialists in a jargon that is bewildering to a novice, and sometimes even to a veteran geneticist working with evolutionarily distant organisms. For such readers what is needed is a written introduction to the morphology, life cycle, reproductive behavior, and culture methods for the species in question. What are its particular advantages (and disadvantages) for genetic study, and what have we learned from it? Where are the classic papers, the key bibliographies, and how does one get stocks of wild type or mutant strains? Lists giving the symbolism and descriptions for selected mutants that have been retained and are thus available for future studies are provided whenever possible. Genetic and cytological maps, mitotic karyotypes, and haploid DNA values are also included when available.

The chapters in this volume deal with invertebrate species that are favorites of geneticists. Attempts to obtain a chapter dealing with the genetics of *Caenorhabditis elegans* proved unsuccessful. Therefore, the volume begins with a survey of molluscan species that have been studied genetically and then turns to the Insecta, with *Blattella germanica* representing the hemimetabolous species. Next come representatives of certain holometabolous orders (for the Lepidoptera, *Bombyx* and *Ephestia*; for the Coleoptera, *Tribolium*; and for the Hymenoptera, *Apis*,

*Habrobracon* and *Mormoniella*). The remaining chapters concern dipterans of genetic interest. Among these are species famous for their giant polytene chromosomes (*Rhynchosciara*, *Sciara*, *Chironomus*, and *Glyptotendipes*) and species of great importance to human and veterinary medicine (*Anopheles*, *Aedes*, *Culex*, *Musca*, and *Lucilia*). Eleven chapters are devoted to the invertebrate for which the greatest amount of genetic information is available, *Drosophila melanogaster*, and five chapters deal with other species belonging to the same genus.

I am particularly grateful for the splendid assistance provided by Pamela Khipple and Lisa Gross during the preparation of this volume. Volume 4 will cover the vertebrates of genetic interest.

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**PART G**  
**MOLLUSCS OF**  
**GENETIC INTEREST**



# 1

## 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<sup>a</sup>


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

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TABLE 1. Continued

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

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\* 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., *Calyptrea*) 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