PHYSIOLOGY OF MOLLUSCA

EDITED BY

KARL M. WILBUR and C. M. YONGE

VOLUME I

PHYSIOLOGY OF MOLLUSCA

Edited by

KARL M. WILBUR
DEPARTMENT OF ZOOLOGY
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA

C. M. YONGE
DEPARTMENT OF ZOOLOGY
UNIVERSITY OF GLASGOW
GLASGOW, SCOTLAND

VOLUME I

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PHYSIOLOGY OF MOLLUSCA

A Treatise in Two Volumes

Contributors to Volume I

E. J. Denton

V. Fretter

A. Graham

G. Hoyle

W. Russell Hunter

J. E. Morton

G. E. Newell

J. A. C. Nicol

Gareth Owen

C. P. Raven

James D. Robertson

P. R. Walne

Karl M. Wilbur

C. M. Yonge

Contributors

Numbers in parentheses indicate the pages on which the authors' contributions begin.

E. J. DENTON, Marine Biological Laboratory, Plymouth, England (425)

V. FRETTER, Department of Zoology, University of Reading, Reading, England (127)

A. GRAHAM, Department of Zoology, University of Reading, Reading, England (127)

G. HOYLE, Department of Biology, University of Oregon, Eugene, Oregon (313)

W. RUSSELL HUNTER,* Department of Zoology, University of Glasgow, Glasgow, Scotland (83)

J. E. MORTON, Department of Zoology, University of Auckland, Auckland, New Zealand (1, 383)

G. E. NEWELL, Department of Zoology, Queen Mary College, University of London, London, England (59)

J. A. C. NICOL, Marine Biological Laboratory, Plymouth, England (353)

GARETH OWEN, Department of Zoology, University of Glasgow, Glasgow, Scotland (211)

C. P. RAVEN, Zoological Laboratory, University of Utrecht, Janskerkhof, The Netherlands (165)

JAMES D. ROBERTSON, Department of Zoology, University of Glasgow, Glasgow, Scotland (283)

P. R. WALNE, Fisheries Experiment Station, Conway, North Wales (197)

KARL M. WILBUR, Department of Zoology, Duke University, Durham, North Carolina (211, 243)

C. M. YONGE, Department of Zoology, University of Glasgow, Glasgow, Scotland (1)

* PRESENT ADDRESS: Department of Zoology, Syracuse University, Syracuse, New York.

Preface

Winterstein's monumental "Handbuch der vergleichenden Physiologie" published as a series of volumes between 1910 and 1925 reviewed the main features of the physiology of molluscs. Since that period there has been no comprehensive treatment of molluscan physiology. Of recent years, the areas of investigation have extended in many directions; the literature is voluminous and, forming an added difficulty, extremely scattered. In the present volume, and in a second which will follow, an attempt is made to give a full and critical survey of this literature. Physiology has been interpreted very broadly in these volumes. In addition to the subdivisions usually found in physiological treatises, chapters are included dealing with the physiological aspects of development (although not with classic embryology), also with ecology in the sea, in fresh waters, and on land, and with behavior and learning in those most highly evolved molluscs, the Cephalopoda. In recognition of the fact that physiology must be firmly based on structure and systematics, a lengthy introductory chapter is provided, based largely on the results of research on functional morphology.

We have felt it necessary to forego the pleasure of the historical approach. The lineages of physiological ideas have, in consequence, usually not been traced. Rather, emphasis has been placed on developments and experimentation of recent years. So as to discover which periods have provided the greater number of contributions to the present volume, we have been interested in making a frequency plot of the distribution of the 1434 references since 1900. There are two peaks: one in the later 1930's when the post First World War interest in comparative physiology had reached a climax, the other in the mid-1950's when the effect of resumption of disinterested scientific investigation following the Second World War had presumably had its effect. Of the reported studies, 54% are more recent than 1950.

The Mollusca constitute a phylum of unusual interest. Built on a relatively simple (although possibly secondarily simplified) ground plan, they display a range of adaptive radiation unparalleled outside the Arthropoda and the Chordata. They possess a remarkable degree of plasticity; in no other phylum are there so many instances of convergence. The success of the Mollusca has been due to the efficiency of their various, and often characteristic, organ systems and it is with this success that these volumes are primarily concerned. So great are the structural and functional divergences within the phylum that workers on the Gastropoda, on the Bivalvia, and on the smaller molluscan classes may not be conversant with the investigations of those who study the more highly organized Cephalopoda, and the converse may also be true. We would hope that in the present volumes all groups of malacologists would find common meeting grounds.

As Editors, we hope that this volume will be of service to many: to the comparative physiologist who seeks similarities and differences in function, to the cellular biologist who finds particularly suitable material in the nerves, muscles, and other tissues of the Mollusca, to the ecologist for whom physiology is increasingly important, and to the many who are interested in the Mollusca for systematic or economic reasons or just because they are fascinated by these remarkable animals. To others—advanced undergraduates, graduate students, established investigators in various disciplines—we would wish to introduce molluscan physiology as a stimulating field of study with a wealth of experimental material especially suitable for experimentation on a variety of physiological parameters.

We both owe a deep debt of gratitude to our collaborators and first of all to our authors who with understanding and patience have kept their chapters current during the inevitably slow development of this first volume. One of us (K.M.W.) wishes to record his gratitude to Dr. Elizabeth A. McMahan for her indefatigable editorial services, to Mrs. Dorothy S. Fry and Mrs. Ann M. Ellington for their services with manuscripts and bibliographies; and also to the Office of Naval Research and the National Institutes of Health for financial support of experimental studies and the preparation of manuscripts. The other (C.M.Y.) has to record his indebtedness to his research assistant, Miss J. I. Campbell, for help with figures and especially with the systematic index and to his secretary, Miss M. McDill, for continued help in the preparation of manuscripts and with endless correspondence. We also acknowledge a most pleasant collaboration with Academic Press.

K.M.W.
C.M.Y.

January, 1964

CONTENTS

Classification and Structure of the Mollusca

J. E. Morton and C. M. Yonge

Physiological Aspects of the Ecology of Intertidal Molluscs

G. E. Newell

Physiological Aspects of Ecology in Nonmarine Molluscs

W. Russell Hunter

Reproduction

V. Fretter and A. Graham

Development

C. P. Raven

The Culture of *Marine Bivalve Larvae*

P. R. Walne

Growth

Karl M. Wilbur and Gareth Owen

Shell Formation and Regeneration

Karl M. Wilbur

Osmotic and Ionic Regulation

James D. Robertson

Muscle and Neuromuscular Physiology

G. Hoyle

Special Effectors: Luminous Organs, Chromatophores, Pigments, and Poison Glands

J. A. C. Nicol

Locomotion

J. E. Morton

The Buoyancy of Marine Molluscs

E. J. Denton

CHAPTER 1

Classification and Structure of the Mollusca

J. E. Morton
DEPARTMENT OF ZOOLOGY, UNIVERSITY OF AUCKLAND, AUCKLAND, NEW ZEALAND

C. M. Yonge
DEPARTMENT OF ZOOLOGY, UNIVERSITY OF GLASGOW, GLASGOW, SCOTLAND

Part 1. Classification

I. Class Monoplacophora

Typified living by *Neopilina* (order Tryblidiacea). Almost bilaterally symmetrical molluscs, with a ventral foot, and median posterior anus. The mantle completely covered by a single-piece oval shell, and the mantle cavity is a shallow space containing five pairs of uniseriate branched branchiae. Dorsolateral and ventral coelomic cavities are relatively well developed. The auricles are in two pairs, the gonads two-paired, discharging through two of the six pairs of renal organs. The nervous system is primitive with longitudinal pallial and pedal cords.

II. Class Amphineura

Elongated, bilaterally symmetrical molluscs with mouth and anus terminal. Mantle very extensive covering the dorsal surface and sides. Heart dorsal and posterior with ventricle and lateral auricles. Nervous system with longitudinal (ganglionic) pallial and pedal cords with cross anastomoses.

A. Subclass Polyplacophora

Flattened littoral or sublittoral Amphineura with a broad ventral foot; the mantle bearing eight transverse shell plates, bordered by a spiculose or scaly girdle. Ctenidia multiplied into numerous pairs, adjacent ones functionally associated so dividing each pallial groove into anterior and outer inhalant, and posterior and inner exhalant, cavities. Characteristically intertidal.

B. Subclass Aplacophora

Aberrant worm-like elongated Amphineura with the mantle completely investing the body, save for a longitudinal ventral groove (in Neomeniomorpha) containing a linear vestige of the foot. The mantle is studded with numerous calcified spicules. Living in deeper water, feeding upon deposits in ooze (Chaetodermomorpha) or on corals and hydroids (Neomeniomorpha).

III. Class Gastropoda

Asymmetrical Mollusca with a well-developed head and, at least primitively, a broad flattened foot. The shell is in one piece, coiled in a helical spiral, at least in the young stages. The visceropallium has undergone torsion of 180°; because of its asymmetrical coiling (distinct from torsion) the palliopericardial complex is usually reduced and one-sided.

A. Subclass Prosobranchia

Generally aquatic gastropods with the visceral mass retaining pronounced torsion and the visceral loop crossed into a figure of eight. The head carries a single pair of tentacles with eyes at the base. The spiral shell is closed by an operculum. The mantle cavity contains primitively two ctenidia but usually there is reduction to one (posttorsional left). The heart is posterior to this. The solitary gonad opens on the right, either through the right kidney (where the left one is suppressed) or through the renal duct (where the left kidney is retained and functional). In the latter case the genital ducts become elaborate. Usually a free-swimming veliger larva.

1. Order Archaeogastropoda

Prosobranchs often with indications or more of original bilateral symmetry, most primitively with two ctenidia but even where reduced to one, always bipectinate (aspidobranch). The Patellacea (limpets) with one ctenidium (Acmaeidae), with secondary gills in the pallial grooves (Patellidae), or without gills (Lepetidae). Heart with two auricles (diotocardiate), right renal organ always a functional kidney but also conveying genital products, fertilization being external. Nervous system little concentrated.

1a. Order Neritacea

Distinct from Archaeogastropoda owing to enlargement of left renal organ which becomes the functional kidney; right organ lost apart from the duct which becomes incorporated in the genital tract (i.e., as in Mesogastropoda). In consequence males possess a cephalic penis and females a glandular genital tract, hence internal fertilization and egg capsules. In further consequence, unlike Archaeogastropoda, have extensively invaded fresh water and land.

2. Order Mesogastropoda
Organs of right side of palliopericardial complex lost. Ctenidium monopectinate (pectinibranch), osphradium well-developed, sometimes pectinate. Nervous system more concentrated. Left kidney alone functional, genital products conveyed via former right kidney duct with pallial glandular extensions producing egg capsules or jelly mass. Cephalic penis and internal fertilization. Usually a free-swimming veliger. Shell sometimes siphonate, carnivorous habit with eversible proboscis in some.

3. Order Neogastropoda
Most advanced Prosobranchia, with highly concentrated nervous system, a siphonate shell, and eversible proboscis. Carnivorous habits, feeding on living or dead animals. Free-swimming veliger usually suppressed, with embryos as a rule intracapsular, sometimes practicing embryonic cannibalism. Osphradium large, bipectinate.

B. Subclass Opisthobranchia
Marine hermaphrodite Gastropoda; shell reduced, becoming internal and finally disappearing with an accompanying tendency to detorsion, the mantle cavity moving back along the right side and widely opening before final loss; also uncrossing and shortening of the visceral loop. Gill probably never a ctenidium. Calcareous spicules often developed in notum of naked forms. With loss of torsion and of asymmetrical shell, eventual return to bilateral external symmetry, with great adaptive range of form and color, feeding, and locomotion. Usually with a (reduced) free-swimming veliger.

1. Order Cephalaspidea (Bullomorpha)
Shell moderately large and pallial cavity well-developed, with a single plicate gill. Head forming a large shield for burrowing. Parapodia prominent and sometimes fin-like.

2. Order Anaspidea (Aplysiomorpha)
Shell reduced and internal, mantle cavity a small recess on right side. No head shield; animals crawling or swimming by enlarged parapodia.

3. Order Thecosomata
Planktonic pteropods with parapodial fins, with a spirally coiled shell, or a modified nonspiral "pseudoconch." Pallial cavity well-developed.

4. Order Gymnosomata
Naked planktonic pteropods with small ventral parapodial fins. No shell or mantle cavity, externally symmetrical, and fast-swimming.

5. Order Notaspidea (Pleurobranchomorpha)
Shell reduced and internal, no mantle cavity, but a naked gill overhung by the mantle on the right side. Becoming flattened, slug-like, and externally almost symmetrical.

6. Order Acochlidiacea
Tiny interstitial sand-dwelling opisthobranchs, visceral mass marked off as a long hump from the foot, without dorsal appendages, though with spicules.

7. Order Sacoglossa
Herbivorous suctorial opisthobranchs with characteristically modified radula and buccal mass. Running from primitive shelled and spirally coiled forms to slug-like "nudibranchs."

8. Order Acoela (Nudibranchia)
Naked, externally almost symmetrical slugs, no mantle cavity or external shell. Dorsal integument with outgrowths such as cerata, or with pinnate retractile gills encircling a median anus.

C. Subclass Pulmonata

Hermaphrodite Gastropoda, with no ctenidium, with mantle cavity vascularized as a lung. A small contractile pallial aperture. Detorsion seldom complete, but nervous system concentrated to lose all trace of chiastoneury. Shell and visceral mass primitively spiral but may assume slug-like form.

1. Order Basommatophora

Head with a single pair of noninvaginable tentacles with eyes at base; most species aquatic, primitively or by reversion, and may acquire secondary gills.

2. Order Stylommatophora

Two pairs of invaginable tentacles, eyes on summit of hinder pair. Terrestrial snails, giving rise by loss of spiral shell to slugs.

IV. Class Scaphopoda

Marine and bilaterally symmetrical molluscs, mantle and shell elongated, uniting ventrally to form a tapered tube open at either end. Foot cylindrical and pointed. No ctenidium. Head without eyes but carrying paired clusters of food-catching captacula. Sexes separate without special genital ducts. Fertilization external.

V. Class Bivalvia

Bilaterally symmetrical Mollusca with rudimentary head, without radula. Ciliary feeders using labial palps and greatly enlarged ctenidia. Two mantle lobes enclosing laterally compressed body and secreting single shell consisting of two calcified valves and a dorsal ligament which, usually together with teeth formed from the valves, constitutes the hinge. Compressed foot adapted for burrowing, without plantar surface. Fertilization external; usually long larval life.

A. Subclass Protobranchia

Ctenidia with flat, nonreflected filaments, hypobranchial glands retained. Foot opening out to expose flattened ventral surface and with numerous retractors. Apart from Solemyidae, feeding primarily by means of extensile "proboscides" from enlarged labial palps. With primitive but also some very specialized characters.

B. Subclass Lamellibranchia

Ctenidia much larger relative to palps and forming feeding organs; filaments greatly elongated and reflected, forming two-sided lamellae the arms being usually united by lamellar junctions. Adjacent filaments attached by ciliary junctions (filibranch condition) or united by tissue (eulamellibranch condition).

1. Order Taxodonta

Gill filaments free and without interlamellar junctions. Mantle lobes free throughout, anterior and posterior adductors subequal. Hinge with numerous similar teeth.

2. Order Anisomyaria

Gills usually filibranch with vascular interlamellar junctions. Byssal fixation leading to diminution of anterior adductor, giving rise eventually to monomyarian condition with radical rearrangement of symmetry leading sometimes to cementation (e.g., Ostraeidae), sometimes to freedom (e.g., many Pectinidae). Apart from separation of exhalant aperture, mantle open; foot small (sometimes absent) and usually without siphons.

3. Order Heterodonta

Gills eulamellibranch and shell less modified than in Anisomyaria, with adductors similar. Hinge dentition is of the "heterodont" type. Mantle edges usually united at one or more points ventrally, and often produced posteriorly into siphons. Shallow or deep-burrowing, or occasionally surface-living.

4. Order Schizodonta
Gills eulamellibranch but probably an artificial group, associating, by virtue of their similar "schizodont" hinge, marine Trigoniacea and freshwater Unionacea.

5. Order Adapedonta
Eulamellibranch gills, and the mantle margins completely closed ventrally save for pedal gape. Siphons long and united; the gills may extend into them. The ligament is weak or wanting and the shell gaping. Deep and permanent burrowing, often penetrating hard substrata.

6. Order Anomalodesmata
Eulamellibranch gills, the mantle edges extensively fused. Hinge teeth lacking. Foot small, external gill plate directed dorsally, Hermaphrodite, with separately opening ovary and testis.

C. Subclass Septibranchia
Adductors equal; mantle edges not extensively fused. Gills transformed into a muscular septum pumping water through the mantle cavity. Macrophagous, feeding, often at considerable depth, upon animal remains.

VI. Class Cephalopoda
Bilaterally symmetrical Mollusca with circle of tentacles round the head. Circulation in the mantle cavity reversed with epipodium modified to form a pallial funnel through which passes the concentrated exhalant current which serves for jet propulsion. Nervous system greatly concentrated and highly organized sense organs. Of higher metabolism than other Mollusca.

A. Subclass Nautiloidea
Extinct save for genus *Nautilus,* but formerly very numerous. An external, many-chambered siphunculate shell, coiled or straight. Head with numerous tentaculate appendages, retractile, and lacking suckers. Funnel of two separate folds. Ctenidia and renal organs increase to two pairs. Eyes open without cornea or lens.

B. Subclass Ammonoidea
A vast extinct group, in general comparable with and radiating parallel to the Nautiloidea. Of the structure of the animal, little can be reliably known.

C. Subclass Coleoidea
In living forms the mantle is naked and forms a sac covering the viscera and containing a more or less rudimentary shell. The head has always eight sucker-bearing arms, and there may be in addition a pair of longer and retractile tentaculate arms between the third and fourth short pairs. Funnel always a closed tube. Ctenidia and renal organs a single pair. Eye with a crystalline lens and closed or open cornea. Ink sac present.

1. Order Decapoda
Tentacular retractile arms in addition to eight normal arms which are shorter than the body. Suckers pedunculate with horny rings. Internal shell relatively well-developed. Squids and cuttlefish. Teuthoidea, Sepioidea.

2. Order Octopoda
Eight uniform arms longer than the body, with nonpedunculate suckers. The mantle encloses the viscera in a rounded muscular sac, and the internal shell is lacking, although the female *Argonauta* has an external "shell" secreted by the dorsal arms. Polypoidea, Cirroteuthoidea.

3. Order Vampyromorpha
"Vampire squids," now separated from Octopoda by differences in the

arm pattern; eight long arms united by a swimming web and two small, retractile, tendril-like arms.

Part 2. Basic Anatomy

I. PRIMITIVE MOLLUSCA

The first molluscs were probably flat-bodied animals crawling on a flat sole. Judging from the basic shape and locomotion of the most primitive existing forms, affinities, although distant, were closest to the Turbellaria. Despite *Neopilina*, there would seem to be no advantages and formidable obstacles to linking the molluscs with any worm visibly metamerically segmented. Certainly, if *Neopilina* displays primitive structure, then a major secondary simplification must have preceded the evolution of the other molluscan classes. The early anteroposterior axis was in line with the foot and there was complete bilateral symmetry with mouth anterior and anus posterior. The head carried sensory tentacles and perhaps eyes. The snout was carried close to the ground, particulate matter being scraped by a protrusible radula. Initially, both feeding and locomotion were probably muscular activities with other functions performed by cilia and mucus secretion.

Early in the molluscan evolution a second, dorsoventral, growth axis appeared. The viscera became concentrated within a dome-shaped protuberance carried on the muscular foot. This *visceropallium*, which constitutes the second recognizable element of molluscan design, was covered by a secreting epithelium, the *pallium* or *mantle*, which extended peripherally to overlap the foot. This secreted the protective shell, initially probably noncalcareous, and both mantle and shell grew radially by marginal increment. Many complexities of molluscan form can best be understood by reference to the interacting symmetries of the head-foot (bilateral) and of the visceropallium (radial or biradial).

Series of shell muscles (Fig. 1), inserted some distance from the margin of the shell and radiating into the substance of the foot, attached the visceropallium to the head-foot and enabled the shell to be drawn down against the substratum.

As recently stressed by Fretter and Graham (1962) in their "British Prosobranch Molluscs" (a book of great importance), the original molluscan *pallial cavity* not improbably consisted of a groove between mantle skirt and foot into which kidneys and anus opened and which housed paired series of gills (possibly prectenidia). But further molluscan evolution followed its great posterior enlargement with formation of a combined respiratory and cloacal chamber into which an enlarged foot could be withdrawn.