Reproductive Biology of Invertebrates

VOLUME I
Oogenesis, Oviposition, and Oosorption

Edited by
K. G. Adiyodi and
R. G. Adiyodi

REPRODUCTIVE BIOLOGY OF INVERTEBRATES

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A Wiley–Interscience Publication

JOHN WILEY & SONS
Chichester . New York . Brisbane . Toronto . Singapore

Library of Congress Cataloging in Publication Data:
Main entry under title:
Reproductive biology of invertebrates.

'A Wiley–Interscience Publication.'
Includes index.
Contents: v. 1. Oogenesis, oviposition, and oosorption.
1. Invertebrates—Reproduction. I. Adiyodi, K. G., 1937–. II. Adiyodi, Rita G. [DNLM: 1. Invertebrates. 2. Reproduction. QL 364 R425]
QL364.15.R45 592'.016 81–16355
AACR2

ISBN 0 471 10128 1

British Library Cataloguing in Publication Data:

Reproductive biology of invertebrates.

Vol. 1: Oogenesis, oviposition, and oosorption
1. Invertebrates—Reproduction
I. Adiyodi, K. G. II. Adiyodi, Rita G.
592'.016 QL364.15

ISBN 0 471 10128 1

Photosetting by Thomson Press (India) Limited New Delhi and
Printed and bound in Great Britain at The Pitman Press, Bath

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Volume V	SEXUAL DIFFERENTIATION AND BEHAVIOUR
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SERIES PREFACE

Invertebrates surpass vertebrates not only in the number of species (as many as 95 per cent of all known animals are invertebrates) and individuals but also in the diversity of structure, adaptations, reproductive biology, sexual behaviour, and development. Reproductive biology is central to all biology, and that of invertebrates has great applied value in management of the myriads of species that are economically useful to man or are harmful to him and his crops and livestock, apart of course from its theoretical and phylogenetical interest. Our knowledge of various aspects of reproduction of invertebrates is, however, not very satisfactory compared to that of vertebrates. Among invertebrates, insects, crustaceans, molluscs, polychaete annelids, and echinoderms have been studied in more detail than other groups, and indeed, very little is known of sexuality, reproduction, and development of some groups such as the Kinorhyncha and Nematomorpha. The unevenness in our knowledge on reproduction of invertebrate groups seems only to become accentuated as the years pass by, for the tendency is to research increasingly into areas that have been more frequently investigated. The information on invertebrate sexuality, reproduction, and development is widely scattered in a multitude of journals over a time span of approximately one century; obviously, it is difficult for the individual investigator to have access to all the literature or to benefit from comparisons with other groups.

It was these circumstances, needs, and compulsions that led us to organize and edit this multivolume treatise on invertebrate reproduction. We have preferred a thematic rather than a phyletic scheme for various volumes in the series, not only because it is in keeping with the current practice of emphasis on systems and processes but also because this arrangement, we felt, is the more suitable one to draw comparisons between different groups and for the chapters to be more authoritative and provocative. Each volume in this treatise is thus independent, but paradoxically enough, also dependent on the others. When information on one group is spread over six volumes, there is a likelihood that overlap might occur between volumes. Overlap has been reduced to the minimum in this series by providing the authors in advance with a subject outline and by careful editing, but some overlap nevertheless does exist, where it has been allowed for purposes of clarity and understanding.

No book is complete, perhaps not even the Scriptures. This is particularly true of books on an almost infinitely diverse and numerically large assemblage as the invertebrates. The present series, 'Reproductive Biology of Invertebrates' is no exception. In spite of our persistent efforts, we did not succeed in commissioning contributions on certain groups to some volumes for various

reasons, a task we have been forced to leave to the future. But what has been competently narrated, overviewed, discussed, and questioned in different volumes of this treatise encompasses a large body of very useful information, some parts of which have not been hitherto available in any form. The authors were encouraged to suggest topics of interest for future research. Many contributors did. Clearly, what is known of invertebrate propagation amounts to only a small fragment of the information that remains to be discovered. We hope that invertebrates, by virtue of their relatively small sizes, easy availability, short reproductive cycles, easy experimental manoeuvrability, great diversity, and exemption from vivisection rules will attract more investigators in the future.

A survey of the information pieced together over the past century on invertebrate sexuality, reproduction, and development shows that the edifice that has been built is based largely on glimpses of only a small number of processes in a surprisingly small number of species. Though this calls for the utmost caution in attempting any broad generalizations, it is tempting to suggest that there may be a common denominator—a common controlling system—at work in regulating sexuality, reproduction, and development in all animals, invertebrate and vertebrate, a system which differs only in details and complexity in different animals, related to their phylogenetic state and ecological needs. It is perhaps logical to assume that biological forces and laws governing propagation of species may be essentially as simple as are the physical forces and laws of nature. We hope this treatise will stimulate future investigators to test the soundness or otherwise of this unified hypothesis.

We are grateful to our contributors for their cooperation, patience, and understanding, and to scientist colleagues, too many to be listed, who offered valuable suggestions and advice and willingly and gladly peer reviewed the manuscripts. We thank most cordially Dr. Janet Boullin who initiated this project at Messrs John Wiley & Sons, Ltd., Chichester in 1978 and Dr. Stephen D. Thornton, Publishing Editor, Life Sciences, who ever since has been the dynamic force behind its completion. We would like to thank the scientific and technical staff and students of the Vatsyayana Centre of Invertebrate Reproduction, Calicut University, for their many kindnesses and help which greatly lessened the burden of the work involved, and it is to them and to our children, Nirmal and Laxmi, who missed many an evening with us which legitimately belonged to them, that this treatise is dedicated most affectionately and warmly.

Calicut University K. G. ADIYODI
R. G. ADIYODI

PREFACE TO VOLUME I

This volume, the first of the two on gametology in this series, 'Reproductive Biology of Invertebrates', deals with the origin, growth, structure, composition, and function of the female gamete and also discusses ovipository behaviour, oosorption, and endogenous and exogenous mechanisms controlling egg production and spawning in invertebrates. Information is also included on morphology, cytology, physiology, and biochemistry of the ovary and the female reproductive tract of several invertebrate groups, but the accessory sex glands associated with the female genital system which provide secretions used in maintenance of the female gamete, formation of egg coverings, and in passage of eggs along the genital duct are only mentioned briefly (for details, see Volume III).

Biochemistry, endocrinology, and ultrastructural aspects of vitellogenesis have been active areas of research in recent years, particularly in view of the finding that in crustaceans, insects, and perhaps also polychaete annelids, vitellogenins synthesized extraovarially constitute part or bulk of the lipovitellins of eggs as in fishes, amphibians, and birds. In other invertebrates in which eggs are produced in large numbers over relatively short periods (e.g. some molluscs), extraovarian participation in yolk formation may be suspected, though no firm indications have been available to date. With regard to protein yolk biosynthesis, the invertebrates are autosynthetic, heterosynthetic, or both; in the mixed type of biosynthesis, the degree of preponderance of one mode over the other varies not only between groups but even within groups. Though phylogenetic conclusions on heterosynthetic ability are premature in the present state of our knowledge, it is clear both schizocoelomate protostome and deuterostome stocks of Bilateria have some groups whose oocytes have acquired the ability to incorporate proteinaceous yolk from without. It would be worthwhile to look for the beginnings of the heterosynthetic process further down in invertebrate history.

Composition of yolk varies with groups and also within groups. In any case, yolk is not all protein: the contributors to this volume have also provided information, wherever feasible, on carbohydrate and lipid components of the yolk and their formation, but this is clearly an area where more critical work is desirable. Vitellus has been considered here as comprising all kinds of yolk and not merely the proteinaceous yolk. The recent tendency in some quarters to restrict the use of the term 'vitellogenesis' to formation of only the proteinaceous type of yolk is to be deprecated. We have dropped the oft-used term, 'previtellogenesis' as it is confusing; in several instances, the so-called 'previtellogenic' oocytes do contain yolk! We have instead preferred to use the

term, 'early vitellogenesis' or 'primary vitellogenesis' to describe the first phase of vitellogenesis, and the term 'secondary vitellogenesis' for the subsequent phase when yolk is deposited faster and in larger amounts.

Reproduction cannot be seen as a process in isolation. Oogenesis which often involves considerable investment in terms of energy is, as far as possible, temporally separated from other high-energy-demanding processes like growth, though in some groups such as natantian decapods, amphipods, and cirripedes, both processes may go on almost hand in hand. Implications of the relationship between growth and reproduction are discussed here in polychaete annelids, myriapods, and crustaceans with special reference to oogenesis; some insight is also given on the endocrine basis of this relationship.

Though some of the very essential features of oogenesis, such as the cytology of maturation divisions, have remained almost the same throughout the animal kingdom, differences exist among various groups in details of structure, chemistry, and physiology of the female gamete and its spawning behaviour; some of these are of course associated with evolutionary history, whereas others are directly traceable to varied demands imposed by the habitat and life cycle. Contributors to this volume have described this diversity in some detail and tried to analyse its meaning and mechanisms.

K. G. ADIYODI
RITA G. ADIYODI

SYSTEMATIC RÉSUMÉ OF THE INVERTEBRATES

Phylum Porifera

- Class Hexactinellida (*Farrea*, *Euplectella*)
- Class Calcarea
  - Subclass Calcinea (*Clathrina*, *Ascandra*)
  - Subclass Calcaronea (*Sycon*, *Grantia*)
  - Subclass Pharetronida (*Neocoelia*)
- Class Demospongiae
  - Subclass Homoscleromorpha (*Oscarella*)
  - Subclass Tetractinomorpha (*Geodia*, *Tetilla*)
  - Subclass Ceractinomorpha (*Halichondria*, *Haliclona*)

Phylum Cnidaria (Coelenterata)

- Class Hydrozoa
  - Order Hydroida (*Hydra*, *Obelia*)
  - Order Milleporina (*Millepora*)
  - Order Stylasterina (*Stylaster*, *Allopora*)
  - Order Trachylina (*Geryonia*, *Cunina*)
  - Order Siphonophora (*Halistemma*, *Physalia*)
- Class Scyphozoa
  - Order Stauromedusae (*Lucernaria*, *Haliclystus*)
  - Order Cubomedusae (*Carybdea*, *Chiropsalmus*)
  - Order Coronatae (*Nausithoe*, *Periphylla*)
  - Order Semaeostomeae (*Aurelia*, *Cyanea*)
  - Order Rhizostomeae (*Rhizostoma*, *Cassiopeia*)
- Class Anthozoa
  - Subclass Octocorallia (Alcyonaria)
    - Order Stolonifera (*Tubipora*, *Cornularia*)
    - Order Telestacea (*Telesto*, *Coelogorgia*)
    - Order Alcyonacea (*Alcyonium*, *Heteroxenia*)
    - Order Coenothecalia (*Heliopora*)
    - Order Gorgonacea (*Corallium*, *Gorgonia*)
    - Order Pennatulacea (*Pennatula*, *Renilla*)
  - Subclass Hexacorallia (Zoantharia)
    - Order Actiniaria (*Edwardsia*, *Lebrunia*)
    - Order Corallimorpharia (*Corynactis*)

Order Scleractinia (*Cladocora*)
Order Zoanthidea (*Zoanthus*, *Palythoa*)
Order Antipatharia (*Schizopathes*, *Dendrobrachia*)
Order Ceriantharia (*Cerianthus*)

Phylum Ctenophora

Class Tentaculata
Order Cydippida (*Mertensia*, *Pleurobrachia*)
Order Lobata (*Bolinopsis*, *Leucothea*)
Order Cestida (*Cestum*, *Velamen*)
Order Platyctenea (*Coeloplana*, *Ctenoplana*)
Class Nuda
Order Beroida (*Beroë*)

Bilateria: Protostomia

ACOELOMATA

Phylum Platyhelminthes

Class Turbellaria
Group Archoophora
Order Nemertodermatida (*Meara*, *Nemertoderma*)
Order Acoela (*Diopisthoporus*, *Childia*)
Order Catenulida (*Stenostomum*, *Catenula*)
Order Macrostomida (*Macrostomum*, *Promacrostomum*)
Order Polycladida (*Cryptocelides*, *Stylochus*)
Group Neoophora
Order Lecithoepitheliata (*Hofstenia*)
Order Prolecithophora (*Prolecithoplana*)
Order Neorhabdocoela (Rhabdocoela) (*Dalyellia*, *Typhloplana*, *Gyratrix*)
Order Proseriata (*Parotoplana*)
Order Tricladida (*Geoplana*, *Dugesia*)
Class Temnocephalida (*Temnocephala*)
Class Trematoda
Order Monogenea
Suborder Monopisthocotylea (*Gyrodactylus*, *Monocotyle*)
Suborder Polyopisthocotylea (*Polystoma*, *Hexabothrium*)
Order Aspidobothria (Aspidogastrea) (*Aspidogaster*, *Stichocotyle*)
Order Digenea (*Paragonimus*, *Fasciola*, *Schistosoma*)
Class Cestoidea
Subclass Cestodaria
Order Amphilinidae (*Amphilinia*)
Order Gyrocotylidea (*Gyrocotyle*)
Subclass Eucestoda

Order Caryophyllidea (*Hunterella*, *Glaridacris*)
Order Spathebothriidea (*Diplocotyle*, *Spathebothrium*)
Order Trypanorhyncha (Trypanorhynchida) (*Lacistorynchus*)
Order Pseudophyllidea (*Triaenophorus*, *Diphyllobothrium*)
Order Lecanicephalidea (*Lecanicephalum*, *Disculiceps*)
Order Aporidea (*Nematoparataenia*, *Apora*)
Order Tetraphyllidea (*Acanthobothrium*, *Oncobothrium*)
Order Diphyllidea (*Echinobothrium*, *Ditrachybothridium*)
Order Litobothridea (*Litobothrium*)
Order Proteocephalata (Proteocephalidea) (*Proteocephalus*)
Order Cyclophyllidea (*Hymenolepis*, *Taenia*)
Order Nippotaeniidea (*Nippotaenia*)

Phylum Mesozoa

Order Dicyemida (Rhombozoa) (*Dicyema*, *Pseudicyema*)
Order Orthonectida (*Rhopalura*)

Phylum Nemertina (Rhynchocoela)

Subclass Anopla
Order Palaeonemertini (*Cephalothrix*)
Order Heteronemertini (*Cerebratulus*, *Lineus*)
Subclass Enopla
Order Hoplonemertini (*Amphiporus*, *Prostoma*)
Order Bdellonemertini (*Malacobdella*)

Phylum Gnathostomulida

Order Filospermoidea (*Haplognathia*)
Order Bursovaginoidea
Suborder Scleroperalia (*Gnathostomula*)
Suborder Conophoralia (*Austrognatharia*)

PSEUDOCOELOMATA

Phylum Rotifera

Class Seisonidea (*Seison*)
Class Bdelloidea (*Philodina*, *Habrotrocha*)
Class Monogononta (*Asplanchna*, *Platyias*)

Phylum Gastrotricha

Order Macrodasyida (*Macrodasys*, *Turbanella*)
Order Chaetonotida
Suborder Multitubulatina (*Neodasys*)
Suborder Paucitubulatina (*Heteroxenotrichula*)

Phylum Kinorhyncha

Suborder Cyclorhagae (*Echinoderes*, *Echinoderella*)
Suborder Conchorhagae (*Semnoderes*)
Suborder Homalorhagae (*Pycnophyes*, *Trachydemus*)

Phylum Nematoda

Class Nematoda
Subclass Torquentia
Order Monhysterida (*Cylindrolaimus*, *Theristus*)
Order Desmoscolecida (*Desmoscolex*, *Tricoma*)
Order Araeolaimida (*Camacolaimus*, *Bathylaimus*)
Order Chromadorida (*Paracanthonchus*, *Desmodora*)
Subclass Secernentia
Order Rhabditida (*Rhabditis*, *Bunonema*)
Order Tylenchida (*Tylenchus*, *Ditylenchus*)
Order Strongylida (*Strongylus*, *Triodontophorus*)
Order Ascaridida (*Ascaris*)
Order Spirurida (*Thelazia*, *Oxyspirura*)
Subclass Penetrantia
Order Enoplida (*Enoplus*, *Mononchus*)
Order Dorylaimida (*Dorylaimus*, *Actinolaimus*)
Order Trichocephalida (*Trichuris*, *Capillaria*)
Order Dioctophymatida (*Dioctophyme*, *Hystrichis*)

Phylum Nematomorpha

Order Nectonematida (*Nectonema*)
Order Gordiida (*Gordionus*, *Paragordius*)

Phylum Acanthocephala

Order Palaeacanthocephala (*Acanthocephalus*, *Gorgorhynchus*)
Order Archiacanthocephala (*Macracanthorhynchus*, *Moniliformis*)
Order Eoacanthocephala (*Neoechinorhynchus*, *Pallisentis*)

SCHIZOCOELOMATA

Phylum Priapulida (*Priapulus*, *Halicryptus*)

Phylum Sipuncula (*Dendrostomum*, *Golfingia*, *Aspidosiphon*)

Phylum Mollusca

Class Monoplacophora (*Neopilina*)
Class Polyplacophora (*Acanthochiton*, *Lepidochiton*)
Class Aplacophora (*Chaetoderma*, *Neomenia*)
Class Gastropoda

Subclass Prosobranchia
Order Archaeogastropoda (*Haliotis*, *Trochus*)
Order Mesogastropoda (*Littorina*, *Janthina*)
Order Neogastropoda (*Murex*, *Buccinum*)
Subclass Opisthobranchia
Order Tectibranchia (*Bulla*, *Aplysia*)
Order Pteropoda (*Spiratella*, *Clio*)
Order Nudibranchia (*Doris*, *Aeolidia*)
Subclass Pulmonata
Order Basommatophora (*Lymnaea*, *Planorbis*)
Order Systellommatophora (*Vaginulus*, *Laevicaulis*)
Order Stylommatophora (*Helix*, *Deroceras*)
Class Scaphopoda (*Dentalium*, *Cadulus*)
Class Pelecypoda (Bivalvia)
Order Protobranchia (*Nucula*, *Yoldia*)
Order Filibranchia (*Mytilus*, *Ostrea*)
Order Eulamellibranchia (*Mercenaria*, *Teredo*)
Order Septibranchia (*Poromya*, *Cuspidaria*)
Class Cephalopoda
Subclass Nautiloidea (Tetrabranchia) (*Nautilus*)
Subclass Coleoidea (Dibranchia)
Order Decapoda (*Loligo*, *Spirula*)
Order Octopoda (*Octopus*, *Argonauta*)

Phylum Echiura (*Echiurus*, *Urechis*, *Bonellia*)

Phylum Annelida

Class Polychaeta
Subclass Errantia (*Nereis*, *Tomopteris*, *Syllis*, *Eunice*)
Subclass Sedentaria (*Chaetopterus*, *Cirratulus*, *Sabellaria*)
Subclass Archiannelida (*Dinophilus*, *Polygordius*, *Trilobodrilus*)
Class Oligochaeta
Order Lumbriculida (*Lumbriculus*, *Stylodrilus*)
Order Tubificida (*Tubifex*, *Enchytraeus*)
Order Haplotaxida (*Haplotaxis*, *Alluroides*, *Moniligaster*, *Lumbricus*)
Class Hirudinea
Order Acanthobdellida (*Acanthobdella*)
Order Rhynchobdellida (*Glossiphonia*, *Piscicola*)
Order Gnathobdellida (*Hirudo*, *Haemadipsa*)
Order Pharyngobdellida (*Erpobdella*)

Phylum Pogonophora

Class Frenulata
Order Thecanephria (*Diplobrachia*, *Polybrachia*)