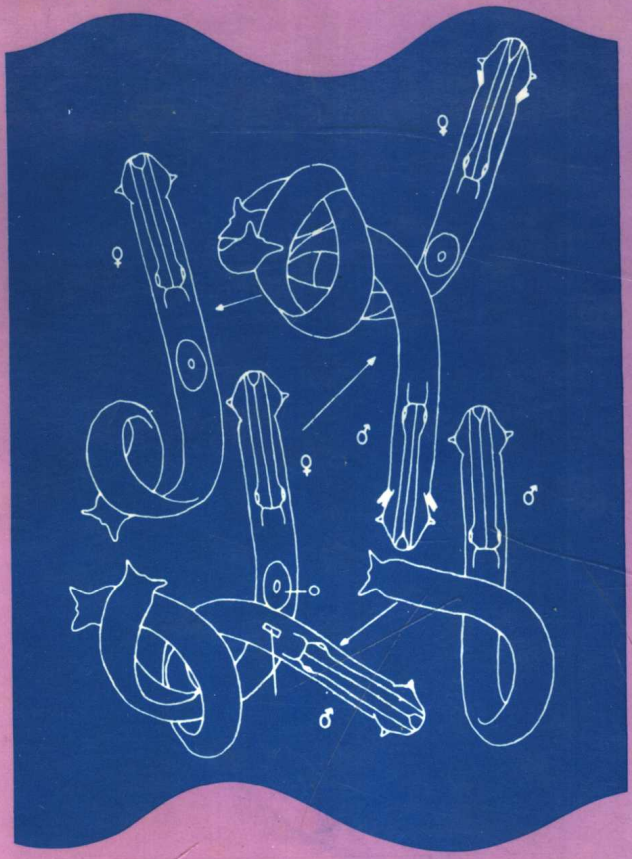
Reproduction of Marine Invertebrates

VOLUME II

ENTOPROCTS AND LESSER COELOMATES



Edited by
Arthur C. Giese
John S. Pearse

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REPRODUCTION OF MARINE INVERTEBRATES

Volume II

Entoprocts and Lesser Coelomates

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GROWTH AND ECOLOGY OF FISH POPULATIONS

By A. H. WEATHERLEY

1972, 300 pp.
ISBN 0–12–739050–2

Growth in fish and its ecological implications has not been evaluated and described in as much detail as other problems related to fish population dynamics. Yet growth is a major connecting link to all these problems. The author believes that a detailed understanding of growth in fish, its sensitive responsiveness to changes in temperature, habitat, food supply, etc., can provide a valuable background knowledge to the ecology of fish populations and can furthermore make a worthwhile addition to general growth biology of animals. The book suggests simple models and schemes for the dissection of such growth processes as production, the relation between growth rate of individual fish and age-specific fecundity, and predator/prey situations. It also outlines possible applications of system analysis for successful attacks on growth problems in the context of populations. This book treats the subject of fish populations from the various standpoints of the ecologist rather than from the more specialized ones of the fishery biologist. In this it is unusual and should appeal not only to fish population biologists but also to animal ecologists in general.

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PREFACE

This volume brings together information on many of the smaller groups of marine metazoans, most of which are difficult to relate to any other group of animals. Each group, however, is of both intrinsic and general interest and should be considered in any broad review of animal reproduction. Some provide favorable material for special studies, for example, the entoprocts with their remarkable asexual capacities. Others, such as the carnivorous pelagic chaetognaths and the interstitial tardigrades, are especially important in particular marine environments. The priapulids, sipunculans, and pogonophorans appear to be related to the annelids and echiurans, and may provide perspective in viewing these important phyla which are considered in Volume III. The hemichordates, and particularly the tunicates and acraniates, are especially interesting in view of their presumed position as predecessors to the vertebrates.

We are indebted to our Advisory Board for suggestions on the scope and organization of the treatise, to the Board and to a larger community of biologists for encouragement and suggestions for additional prospective authors, and to all the authors who enthusiastically assumed responsibility for chapters which required of them much effort and time. We are indebted to Ms. Jean McIntosh for the preparation of the Subject and Taxonomic indexes. Finally, we are indebted to Dr. Vicki Buchsbaum Pearse for her painstaking editorial assistance and to the staff of Academic Press for their help with the development of the treatise.

ARTHUR C. GIESE
JOHN S. PEARSE

CONTENTS OF OTHER VOLUMES

VOLUME I—ACOELOMATE AND PSEUDOCOELOMATE METAZOANS

VOLUME III—ANNELIDS AND ECHIURANS

REPRODUCTION OF MARINE INVERTEBRATES
VOLUME II: ENTOPROCTS AND LESSER COELOMATES

Edited by ARTHUR C. GIESE and JOHN S. PEARSE

This extensive, multivolume treatise is a systematic compilation and synthesis of available information on the reproduction of all groups of free-living, marine, metazoan invertebrates. The treatise contains information previously unpublished as well as existing data. Coverage for each group includes:

- Asexual reproduction (types, influencing factors)
- Sexual reproduction (sexual dimorphism, sex determination and hermaphroditism, anatomy, gametogenesis, gametogenic cycles, behavior, spawning)
- Development (fertilization, embryonic, larvae)

Volume II includes a chapter on the Entoprocta and chapters on eight smaller groups of coelmate metazoans, Tardigrada, Priapulida, Sipuncula, Pogonophora, Chaetognatha, Hemichordata, Acrania and Tunicata. Despite the difficulty in relating these groups of one another, each is of intrinsic interest and affords insight into the process of animal reproduction.

The work will be of value to university, college and marine researchers; professionals and graduate students working in basic and applied research on reproduction, invertebrates, and marine biology; reproductive biologists, invertebrate zoologists and marine biologists.

Jacket design by Jorge Hernandez

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Chapter 1

ENTOPROCTA

Richard N. Mariscal

1.1 Introduction

The Entoprocta (Kamptozoa, Calyssozoa, Endoprocta) comprise a little-known phylum of about 120 species by my count (1971). They are nearly all microscopic, being only a few millimeters in length and are easily overlooked both in the field and in the laboratory.

In spite of their pseudocoelomate nature, for many years they have been included together with the Ectoprocta in the phylum Bryozoa. Because of the presence of a large number of extant species and the extensive ectoproct fossil record, most of the attention paid to the entoprocts has been systematic and by bryozoologists primarily interested in the ectoprocts. For this reason, relatively little modern work has been

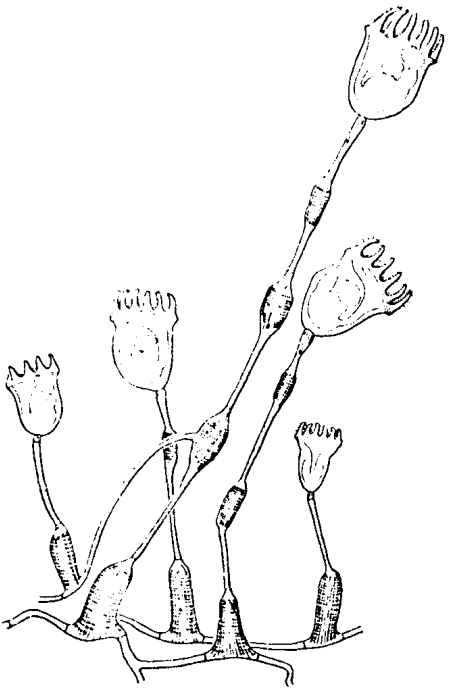

FIG. 1. A portion of a colony of *Barentsia* (probably *B. benedeni*) showing the characteristic muscular swelling at the base of the stalk which distinguishes this genus. This species also may have one or more muscular enlargements along the stalk which allow for the bending of the individual polyp. Note the development of a stolon from one of the muscular nodes on the stalk (from Cori, 1936).

done on entoprocts and much of what we know of their biology comes from several lengthy papers and monographs from the nineteenth and early part of the twentieth centuries.

The basic body plan is similar throughout the phylum. The adult polyps or zooids all consist of a tentacle-bearing, bowl-shaped calyx perched on a long thin stalk which may have bulbous muscular enlargements along its length (Fig. 1). Both mouth and anus are connected by the characteristic **U**-shaped gut, opening within the circlet of tentacles, hence, the name of the phylum (Fig. 2). However, there have been two rather divergent lines of evolution within the group. The point of divergence lies in the nature of the base of the stalk, i.e., whether it is attached to the substrate directly or whether it joins with a ramifying stolon which, at periodic intervals, gives rise to other similar polyps. If the polyp is attached directly to the substrate (i.e., solitary), the species is placed in the family Loxosomatidae (Fig. 3). If the polyps are colonial

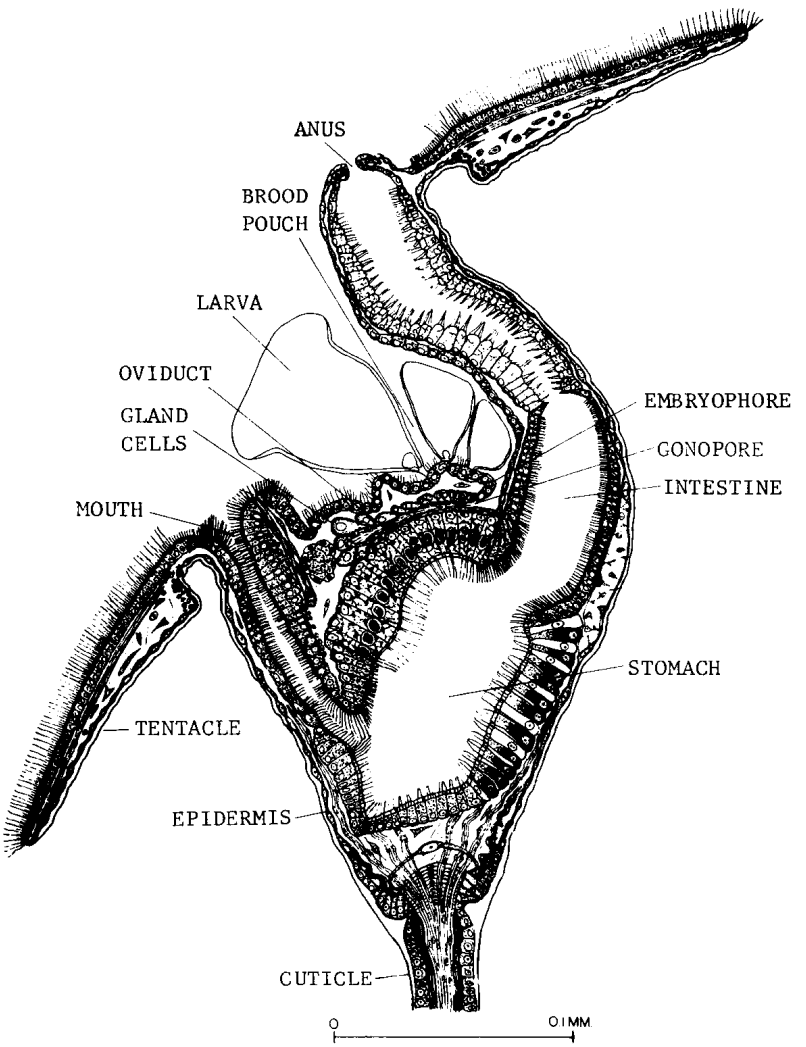

FIG. 2. Median sagittal section of the calyx of an adult female pedicellinid entoproct (*Barentsia benedeni*), showing the relationship of the oviduct, embryophore, brood pouch, and the developing larvae (from Mariscal, 1965).

and interconnected by branching stolons, they belong to the family Pedicellinidae (Fig. 1). A third family is also recognized, the Urnatellidae, which is restricted to fresh water and contains only two species (Fig. 4). The base of the stalk of this form is somewhat intermediate between those of the other two families in that several stalks arise from a single basal

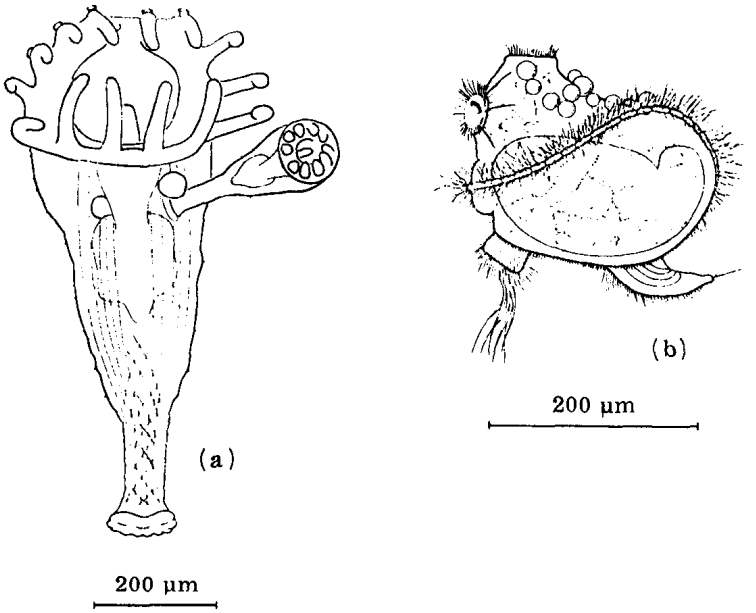

FIG. 3. *Loxosoma jaegersteni.* (a) Adult individual in frontal view. Note the large bud extending from the side of the calyx. (b) *Loxosoma jaegersteni* larva in side view containing an internal bud (from Nielsen, 1966a).

attachment disc. Although higher taxa can be devised, it is convenient and natural to go directly from the phylum to the family level and for that reason the characteristics of the major families and genera will be briefly reviewed.

The solitary Loxosomatidae constitute by far the largest single natural grouping among the Entoprocta. The family is composed of a remarkable collection of largely symbiotic entoprocts which are distinguished by the nature of the foot or attachment organ and the unique development of buds from the calyx. Nearly half of the Loxosomatidae have been found in close association with various families of polychaetes or their tubes. Nielsen (1964a) has summarized much of this information and has listed ten families of Polychaeta with which loxosomatids are known to associate. Although little enough is known about the entoprocts themselves, essentially nothing is known of the biology of this association or the possibilities of any reproductive interaction. In addition, loxosomatids have been found living symbiotically with ectoprocts, sipunculans, sponges, echinoderms, and ascidians, among others. Most of these associations appear to be commensal in nature with the entoproct utilizing

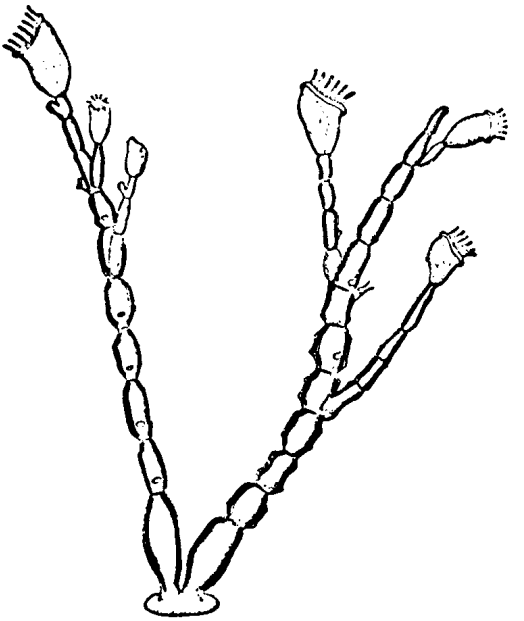

FIG. 4. *Urnatella gracilis* colony showing the beaded stalk and small attachment disc (from Cori, 1936).

the feeding currents and substrate provided, but apparently neither benefiting nor harming the host.

At most, five genera of loxosomatids are currently recognized, the major distinguishing feature being the nature of the foot or pedal attachment organ:

Loxosoma. Basal portion of the stalk of both buds and adults consists of a muscular sucking disc containing scattered glandular cells. The animals are capable of movement on the host throughout life (Fig. 3).

Loxocalyx. Basal portion of the stalk contains a pedal gland, pedal groove, and accessory glandular cells, which are found both in the buds and adults throughout life. Some species, at least, appear capable of movement on the host (Fig. 5).

Loxosomella. Basal portion of the stalk of the buds consists of a foot with a pedal gland and pedal groove with accessory glandular cells. After the bud detaches from the parent it generally becomes permanently cemented to its host and the foot gland degenerates in the adult and may be entirely lost (Fig. 6). Because of the difficulty in clearly distinguishing between the characteristics separating *Loxocalyx*