ASPECTS *of* SPONGE BIOLOGY

Edited by

FREDERICK W. HARRISON

and RONALD R. COWDEN

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To Jeffrey D. Rude
who died October 12, 1975 at McMurdo Sound, Antartica while conducting research on the biology of sponges.

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Preface

Aspects of Sponge Biology developed from a symposium held in Albany, New York, in May 1975, sponsored by the Society for Developmental Biology and the Department of Anatomy, Albany Medical College. This symposium brought together the majority of North American investigators of sponge biology. The book is unusual in that, in addition to presentations in current investigations, it contains the symposium participants' discussion of several of the problem areas of sponge biology. The introductory chapter is intended for established investigators in other fields who either wish to study the sponges *per se* or to utilize these animals as model systems to clarify basic biological problems. This book, then, attempts to present the sponges as a challenging, virtually untapped resource for future studies. It includes the most current research in the field yet, simultaneously, leads investigators into research opportunities seen for the near future. *Aspects of Sponge Biology* should prove valuable to invertebrate zoologist, cell and developmental biologists, aquatic biologists, ecologists, investigators of cell surface phenomena, comparative physiologists, and to anyone involved in problems of water quality. We feel that the study of sponge biology is entering into an extremely exciting and rapidly evolving period in which the utilization of techniques unavailable in the recent past will not only provide answers to many of the problems now existing in sponge biology but will also raise challenging new questions.

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Contents

Introduction and General Discussion

INTRODUCTION: PRINCIPLES AND PERSPECTIVES IN SPONGE BIOLOGY

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Within recent years, the utilization of sponges in research has increased to a tremendous extent. The application of newer technologies to problems of sponge biology has greatly clarified many of the problems that plagued earlier investigators. We feel, however, that the sponges present a virtually untapped tool for use in basic research with many areas of utilization and investigation unrecognized. This chapter is intended, then, to serve as a guide to either the young investigator beginning a career or the established scientist who wishes to utilize, for the first time, sponges as a research vehicle. We realize that it is not possible or reasonable to review all the different facets of sponge biology. However, we wish to introduce the novice to: methods for collecting, laboratory maintenance and examination; key references, including monographs and review papers; and selected areas of research on sponges which need to be undertaken or need to be reevaluated in light of new techniques and/or ideas.

Collecting Techniques

In collecting sponges, the methods employed will often be determined by the collectors' proposed use of the material. If one is collecting for taxonomic studies of marine sponges, for instance, it is best, if feasible, to collect entire specimens. In this case, color photographs, underwater if possible, of the specimens are quite helpful in species determinations. Conversely, with freshwater sponges, the collection of entire specimens is not essential but one should collect gemmule-bearing specimens if possible. This is because most taxonomic schemes in use today employ gemmule and

gemmosclere (gemmule spicule) morphology as diagnostic criteria. In either case, it is important to separate small, five cubic millimeter, pieces of sponge into a histological fixative. Fixatives of preference are Bouins or ethanol-acetic acid (3:1). Following fixation, specimens should be processed routinely through washes, etc., with storage in 70% ethanol. The remainder of the specimen may be placed directly into 70% ethanol or retained as a dried specimen.

Maintenance of Sponges in the Laboratory

The problems of maintenance of marine and freshwater sponges in the laboratory have been reviewed by Fell ('67). Although freshwater sponges are notoriously difficult to maintain in the laboratory, Imlay and Paige ('72) described a simple laboratory system with continuous water flow in which freshwater sponges not only survived for three months but, in most cases, exhibited considerable growth. The continuous flow multichamber system described by these authors used trout fry food (Glencoe starter granules) fed into the first prechamber at the rate of ½ gram of feed per day. Although the exact system described, i.e., direct introduction of raw habitat water, would be impractical for most laboratories, a recirculating system could be easily devised. The design for an inexpensive recirculating system, in this case a refrigerated seawater system for marine organisms, was described by Bakus ('65). This system could be easily adapted for maintenance of freshwater sponges according to the technique of Imlay and Paige ('72).

The various techniques used in laboratory examination of sponges, i.e. explants, dissociation and reaggregation, growth of sponges from larvae, production of sponges from gemmules, and cell culture, have been thoroughly reviewed by Fell ('67) in a particularly informative article.

Current Problems in Systematics

Until recently, the systematics of freshwater sponges was hopelessly confused. The revisionary work of Penney and Racek ('68) brought some degree of order into this chaotic area and, in particular, demonstrated global evolutionary patterns within the gemmule-forming spongillids. However, there are still major areas requiring clarification in freshwater sponge systematics. Traditionally, skeletal and/or gemmule morphology have been the basic criteria utilized in systematic analyses of both freshwater and marine sponges. Increased recognition of the problems caused by ecomorphic variation in skeletal and gemmule structure of spongillids (see Poirrier'69, '74, and this volume) necessitate a more

comprehensive approach. Although non-skeletal characteristics have been utilized in taxonomic studies of marine sponges (see Pomponi, in this volume for a review), their application as diagnostic criteria in freshwater sponge systematics has been limited. Harrison ('71) used cytochemical characteristics in defining one species of spongillid and Arceneaux ('73) applied electrophoretic techniques to problems in freshwater sponge taxonomy, but there has been no significant advance in this area.

Especially in widely distributed freshwater species such as Spongilla lacustris and Eunapius fragilis, possible speciation trends in distant populations should be considered. For example, as Penney and Racek ('68) noted, the majority of sub-artic or cold-temperate forms of S. lacustris show morphological characteristics different from those of more southern forms. While such criteria as the presence or absence of gemmule pneumatic coats (see Poirrier, '69) may reflect ecomorphic variation, there appear to be significant differences in life history, growth forms, etc., in distant populations. As discussions in this volume indicate, speciation trends and the question of subspecific status provide an intriguing area for future research in sponge systematics.

A number of freshwater sponges do not form gemmules and, thus, present special taxonomic problems. Evaluation of the evolutionary relationships of these non-spongillid freshwater sponges has involved the utilization of a number of non-skeletal characters, particularly developmental characteristics (see Brien, '67a, '67b, '70).

It has now become apparent (Brien, '70) that the freshwater sponges are polyphyletic. Recent studies by Racek and Harrison (in preparation) have shown, however, that the various types of freshwater sponges arose from quite a number of ancestors at widely differing times. The clarification of the position of the non-spongillid freshwater sponges will be a major problem - involving clarification of their embryology, ecology, and physiology - inviting further study by systematists for some time to come.

Particularly exciting discoveries, affecting the taxonomy of all sponges have occurred within recent years. During the past 15 years an amazing variety of "living fossil sponges" have been described, all of which possess relatively massive calcareous skeletons. These include Sclerospongiae, (Hartman and Goreau, '70), Sphinctozoa (see Hartman, this volume), and Pharetronida (Vacelet, '70). These discoveries have suggested that the fossil groups, Stromatoporodea and Sphinctozoa, are sponges; furthermore, the Chaetetida have been transferred from the Phylum Cnidaria to the Porifera (Hart-

man and Goreau, '72). Due to the profound effects which these discoveries may have on our view of the phylogeny of the Porifera it is becoming increasingly important that a "new systematics" be put forth which encompasses both these new discoveries and previously established fossil groups. Specifically, a new delineation of higher taxa including their possible interrelationships is called for.

The systematics of the class Demospongiae continues to present challenging problems for the establishment of natural relationships within the group. For example, although Lévi's subdivision of the group into the subclasses Ceractinomorpha and Tetractinomorpha (Lévi, '56) has been generally accepted, Bergquist and Hartman ('69) have concluded, on the basis of amino acid patterns, that the latter subclass is difficult to retain in its present context. They further suggest the abandonment of the order Epipolasida. Numerous problems on the family and generic level are also outstanding, some of which are being evaluated through comparative cytology (see Pomponi, this volume; Simpson, '68b). Further approaches include serological and transplant techniques for determining relationships (Connes, et al., '74; Paris, '61) and comparative studies of reproduction (see Chen, this volume, Connes et al., '74; Lévi, '56) for species delineation.

The basic problem in the taxonomy of the Demospongiae is the derivation of a set of criteria upon which to base homologies. Additional, extensive comparative studies are needed before this can be accomplished.

Life Cycle Events

There are at least three types of biological events which are cyclic in many sponges; these include sexual reproduction, gemmule formation and hatching, and tissue regression. The last mentioned involves the loss of the canal system during winter months and its redevelopment in the spring (see, for example Simpson, '68a) or the developmentally similar formation of reduction bodies (Penney, '33; Harrison et al., '75). Little experimental work or insight into this phenomenon is available. A second type of cycle which is apparently universal among sponges is the seasonal production of gametes. Fell ('74a) has thoroughly reviewed the data on this subject. Gilbert et al. ('75) and Gilbert ('74) have recently shown that gamete production in a freshwater species is probably endogenously controlled; that is, it is independent of environmental stimuli. However, from both these and other studies (see Fell, '74a and this volume) it is clear that water temperature can strongly influence the initiation and/or rate of gametogenesis. Much more experimental work

is required to elucidate the underlying biochemical mechanisms which are responsible for the observed cyclic events. The formation and hatching of gemmules in most freshwater and a few marine species is a third kind of cyclic phenomenon in sponges. The formation of gemmules may also be endogenously controlled (Gilbert, '75) but this situation still requires further investigation. Field data on gemmule formation and hatching has recently been interpreted in terms of an interaction between the environment and the physiological condition of the sponge (Simpson and Fell, '74). Gemmule hatching in the laboratory is strongly affected by temperature but it is not clear if it affects hatching in the field (Simpson and Gilbert, '73). The control of hatching and dormancy may involve changes in cyclic nucleotide metabolism (see Simpson and Rodan, this volume).

Silicon Deposition

We are presently very far from an understanding of the basis of silicon deposition. Recent work on siliceous spicule secretion has demonstrated that a central organic filament (axial filament) and surrounding membrane (silicalemma) are present, probably intracellularly. Silicon is apparently transported by the membrane and polymerized within it (Garrone, '69; Simpson and Vaccaro, '74).

Concentric layering of silicon in spicules has been reported (Schwab and Shore, '71) and is apparently due to differences in water content. However, its significance is not understood. A promising approach to the study of silicon deposition is the use of germanium (Elvin, '72; Simpson and Vaccaro, '74) which, in diatoms (Azam et al., '74), has been shown to be a competitive inhibitor of silicon transport. Since the silicalemma is presumably intracellular, the plasmalemma and other cytoplasmic organelles may also be involved in transport. It has been suggested that the morphology of siliceous spicules may be determined by the morphology of the axial filament (Reiswig, '71), in which case silicon deposition can be viewed as involving a two-component system - the silicalemma which transports silicon and the axial filament which determines the geometry of the polymerized silicon. Germanium apparently uncouples these components producing abnormal bulbous spicules (Elvin, '72; Simpson and Vaccaro, '74; Simpson, unpublished).

Some problems in gemmule physiology

Among the many events which ensue during the hatching of sponge gemmules is the opening of the micropyle. The gemmule coat in freshwater sponges contains much collagen (De-