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Bulletin 12

Natural History of the Marine Sponges of Southern New England

by

Willard D. Hartman

PEABODY MUSEUM OF NATURAL HISTORY, YALE UNIVERSITY

BULLETIN 12

Natural History of the *Marine Sponges* of Southern New England

BY

WILLARD D. HARTMAN

Peabody Museum of Natural History
and
Department of Zoology
Yale University

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Dedicated to

PROF. ALEXANDER PETRUNKEVITCH
on the occasion of his eightieth birthday,
22 December 1955

CONTENTS

ABBREVIATIONS

AMNH—American Museum of Natural History

MCZ—Museum of Comparative Zoology, Harvard College

YPM—Peabody Museum of Natural History, Yale University

ABSTRACT

Twelve species of siliceous sponges from Long Island and Block Island sounds are described. Among these are two new species: *Haliclona loosanoffi,* a gemmuliferous, encrusting haliclonid; and *Haliclona canaliculata,* a flat encrusting species with perennial growth. Of previously described species, *Neosperiopsis deichmannae* de Laubenfels is placed in the genus *Isodictya; Chalina arbuscula* Verrill is regarded as a synonym of *Haliclona oculata* (Pallas).

Variations in spicule size correlated with temperature are described in *Haliclona oculata,* in which the variations are geographical, and in *Halichondria bowerbanki* and *Haliclona canaliculata,* in which the variations are seasonal.

The period of larval settling is reported for five sponges. Annual, temperature-correlated variations in the time of larval settling and gemmule formation are described in *Haliclona loosanoffi.*

Experiments on the tolerance of two species of clionids to lowered salinities indicate that *Cliona vastifica* Hancock has a wider range of tolerance than *Cliona celata* Grant. A review of the distribution of these two species reveals that populations of the former have penetrated brackish waters in several parts of the world where they show parallel trends in variation of spicule form. Competition for substrate between the two species is discussed.

PREFACE

Although there is a wealth of literature on the taxonomy of marine sponges, the classification of many groups of these animals remains in a state of confusion. This is true largely because of a reliance upon skeletal characteristics in distinguishing species. For practical reasons, the museum zoologist has no alternative but to regard skeletal characters of primary importance in identification. Yet there are certain families and genera in which species cannot be identified certainly on the basis of skeletal characteristics alone, and in which attempts to do so have led to an unnecessary multiplicity of species. There is some truth in Bidder's (1928) comment that "most of the alleged species have been made because the differences between spicules can be so closely measured and accurately recorded."

Within the family Haliclonidae, e.g., the genus *Haliclona* is a greatly confused one containing a large number of species many of which are doubtless invalid. The difficulty in this case is that the skeleton consists of only one type of spicule (oxeas); the spicules are arranged in networks which vary from unispicular reticulations to polyspicular tracts joined by isolated spicules. The networks and tracts contain variable quantities of spongin as a cementing agent. Burton (1926) studied the skeletal characteristics of a large series of encrusting haliclonids from a two mile stretch of beach at Littlehampton, Sussex, and found that the skeleton varied from a subisodictyal, unispicular meshwork with spongin restricted to the ends of adjacent spicules to an isodictyal skeleton with multispicular tracts enclosed by a delicate spongin sheath. He concluded that all the colonies represented variations of a single species which he, at that time, called *Reniera cinerea.* In the present studies a similar variability in skeletal structure has been demonstrated in *Haliclona oculata.*

But restricting one's attention to a study of variability in the skeletal features of series of museum specimens can sometimes hide valid differences between species. It has become apparent to the present writer that the challenge of unravelling some of the confused synonymies among sponges can be met best through a thorough study of populations in the field. After becoming acquainted with living populations of sponges, species differences are not infrequently recognizable aesthetically (*see* Pantin, 1954) before they can be communicated to others following the application of analytical laboratory methods. Thus, field studies of the Long Island Sound species of *Halichondria* led me to regard it as distinct from *panicea* long before anatomical differences in the dermal skeleton were demonstrable in the laboratory.

Life history studies, too, have aided in separating species in which spicule structure and size fail to be useful. In studying the local populations of encrusting haliclonids, I was inclined at first to classify them as the so-called cosmopolitan species, *Haliclona permollis,* which I knew from literature studies only. Field studies of the annual cycle of the Long Island Sound haliclonids revealed that they die back in late fall and live through the winter as gemmules, a habit unknown in *permollis.* During the course of a recent reëxamination of the local haliclonids, I became aware of some specimens which looked different from the more common gemmule-bearing species. These colonies were found to remain alive throughout the winter without forming gemmules. They do undergo a partial internal degeneration, however, losing their choanocytes. It is now clear that two species of *Haliclona* occur sympatrically in the vicinity of New Haven,

neither of them synonymous with *H. permollis*. These species might well have remained undetected if sole reliance had been placed on studies of their highly variable skeletal characters.

In instances where several categories of megascleres occur or where microscleres are present, classification on the basis of skeletal characteristics is more certain. But here again environmental factors may have an effect on the spiculation, as has been shown by Jewell (1935) in her ecological studies of spongillids and by Jørgensen's experimental work (1944). These authors found microscleres more sensitive than megascleres to reduced concentrations of silicon. Several instances of variations in spicule form apparently correlated with environmental factors are reported in the present studies. The spicules of *Haliclona oculata* increase in size in colder waters; those of an encrusting haliclonid and a *Halichondria* found in Long Island are larger in winter specimens. The occurrence of parallel variations in spicule form in brackish water populations of *Cliona vastifica* in various parts of the world suggests a correlation with low salinity. In none of these cases, however, has experimental work been carried out as yet to ascertain which of the spicule form variations are ecophenotypic and which genetically determined.

Embryological and biochemical data have also proven applicable to problems of sponge systematics. Topsent (1911) found a difference in breeding seasons and in larval structure in the difficult species, *Halichondria panicea* and *bowerbanki;* Tuzet (1948) has presented sound evidence for the distinctness of the calcareous sponge genera, *Leucosolenia* and *Clathrina*, on the basis of her studies of the early developmental stages of these forms; Lévi (1953a, 1956) has found that larval characteristics are the best ones for separating sibling species of *Halisarca.*

Bergmann's studies (1949) of the sterols of sponges are helpful in defining the families Suberitidae and Spirastrellidae and provide a possible basis for a reëxamination of the genus *Haliclona.* It is probable that biochemical studies of the components of the organic skeletal elements in sponges will yield results of importance to understanding the classifications and phylogeny of the Porifera as they have among the Anthozoa (*see* Roche and Tixier-Durivault, 1951).

The present studies concern the systematics and some ecological relationships of the sponges of Long Island Sound and Block Island Sound. Life history studies of five common species and the salinity tolerances of two sympatric clionids have been investigated with a consideration of the importance of these factors in the distribution of the sponges concerned.

Willard D. Hartman

New Haven, Connecticut
September, 1958

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The late Dr. Stanley C. Ball kindly granted permission to examine the extensive collections of sponges at the Yale Peabody Museum, before I joined the staff of that institution. Dr. Elisabeth Deichmann kindly lent the collection of Woods Hole sponges from the Museum of Comparative Zoology at Harvard College. Dr. John Armstrong permitted me to study specimens from the collections of the American Museum of Natural History.

I am also indebted to Mr. Nathan Bowman, Mr. M. D. Burkenroad, Mr. G. R. Forster, Dr. Claude Lévi, Dr. I. M. Newell, Dr. Max Pavans de Ceccaty, Dr. R. A. Paynter, Jr., Prof. Odette Tuzet, Mr. H. E. Warfel, Dr. D. P. Wilson, and the Director of the Plymouth Laboratory of the Marine Biological Association of the United Kingdom for supplementary collections of sponges made at various places on the Atlantic Coast of North America and in Europe.

Much of the collecting in Long Island Sound was done aboard boats of the Rowe Oyster Company, New Haven, and the Connecticut Oyster Farms, Milford. Collecting in Block Island Sound was done aboard Capt. Ellery Thompson's boat, the "Eleanor."

I am indebted to Dr. Carl O. Dunbar, Director of the Peabody Museum, for helpful criticism in editing of the manuscript. I should also like to express my appreciation to Mr. Frederick Nigretti, formerly preparator in invertebrate zoology at the Peabody Museum, for technical assistance during revision of the manuscript for publication, and to Mrs. Delores McColm for typing and editing the manuscript, and for much helpful criticism. Finally, I am deeply grateful to Miss Shirley P. Glaser for her great care in preparing the figures.

NATURAL HISTORY OF THE MARINE SPONGES OF SOUTHERN NEW ENGLAND

I. SYSTEMATIC STUDIES

PREVIOUS WORK

The material on which these studies are based comprise collections made in rather restricted areas of Long Island Sound and Block Island Sound. The intertidal and shallow water sponge fauna was studied along the Connecticut shore of Long Island Sound from Hammonasset State Park to Milford Point. Deeper water collections were largely restricted to oyster beds ranging from Branford to Bridgeport, Connecticut, down to depths of ten meters and never more than a mile and a half from shore. One collection was made in Clinton Harbor aboard a lobster boat. The northern shore of Long Island, the shore of Connecticut east of Clinton and west of Milford Point, and the deeper central part of the Sound have not been surveyed as yet. Collections from Block Island Sound were made on commercial fishing grounds at depths varying from 20 to 40 meters. It is probable that this fauna penetrates the deeper waters at the eastern end of Long Island Sound.

The above-mentioned collections were supplemented by a few specimens from both Long Island Sound and Block Island Sound in the A. E. Verrill collections at the Peabody Museum.

The earliest study of Long Island Sound sponges was reported by Rafinesque (1819)[1] who described five species from the shores of Long Island Sound. Rafinesque's studies were restricted to the western end of the island, including both the northern Sound shore (Oyster Bay) and the southern shore (Gravesend, Sandy Hook, and Bath [?]). His descriptions are poor and unaccompanied by illustrations. Possible synonyms of his species are:

1. *Spongia albescens* Raf. (whitish sponge) = *Suberites ficus* (Johnston) (?)
2. *Spongia ostracina* Raf. (oyster sponge) = *Microciona prolifera* (E. & S.)
3. *Spongia cespitosa* Raf. (bushy sponge) = *Haliclona oculata* (Pallas)
4. *Spongia cladonia* (cladonian sponge) = *Haliclona oculata* (Pallas) (?)
5. *Spongia virgata* (slender sponge) = *Microciona prolifera* (E. & S.) (?)

Verrill (*in:* Verrill and Smith, 1873) included several Block Island Sound and Long Island Sound records in a report on the invertebrates of Vineyard Sound and adjacent regions. A list of sponges mentioned by him together

[1] Rafinesque regarded sponges as "marine vegetables" since "in all those I have seen, in Europe and America, no perceptible motion nor sensibility was to be discerned in any stage of their existence; and those who have acknowledged their animality, bring no stronger proof thereof than an occasional slight shrinking under the hand, and an animal smell, which are common to some marine plants."

with the occurrence of each species in the waters under consideration follows:

Grantia ciliata Fleming—Rhode Island.
Ascortis fragilis Haeckel—Common in Long Island Sound (New Haven, Thimble Islands); Watch Hill, Rhode Island.
Microciona prolifera Verrill—Abundant in Long Island Sound.
Chalina oculata Bowerbank—Off Watch Hill, Rhode Island, 4—5 fathoms.
Chalina arbuscula sp. nov.—Very common in Long Island Sound; Watch Hill, Rhode Island.
Isodictya (palmata?)—Watch Hill, Rhode Island.
Halichondria panicea Johnston—Abundant off Watch Hill, Rhode Island, on algae in 4—8 fathoms.
Halichondria sp. "a"—Watch Hill, Rhode Island.
Halichondria sp. "b"—Long Island Sound near New Haven.
Halisarca sp.?—Watch Hill, Rhode Island.
Cliona sulphurea Verrill—Very abundant in Long Island Sound on oysters and other shells.

All the species listed except *Halisarca, Halichondria panicea,* and *Halichondria* sp. "a", have been found by the present author in the course of collecting. The synonymies of the species listed by Verrill will be considered in the descriptive section of this paper with the exception of the calcareous sponges which will be discussed in a forthcoming paper.

Verrill (1875) described a "curious, very slender and delicate, bipinnately branched species from the piles both at Greenport and Noank." Specimens of this sponge have not been found in the Peabody Museum and in the absence of data on its skeletal characteristics, one can only guess as to its identity. It is possible that Verrill was referring to colonies of *Haliclona loosanoffi,* a species described as new in the present paper. Verrill goes on to state that "several sponges, new to the fauna [eastern Long Island Sound] were also obtained and were studied by Prof. Hyatt." Unfortunately Hyatt did not publish his studies of these specimens and apparently failed to return them to the Peabody Museum.

Fragments of white Italian marble from a cargo wrecked off Long Island in 1871 were described by Verrill (1878) as being riddled by the boring sponge, *Cliona celata.* The cavities penetrated to a depth of one or two inches.

Old (1941) listed four species of clionids from Long Island Sound: *Cliona celata, C. lobata, C. vastifica,* and *C. truitti.* The first three species have been collected on the Connecticut shores of Long Island Sound, but the last-named species has not been found.

LIST OF DEMOSPONGIAE DESCRIBED FROM LONG ISLAND SOUND AND BLOCK ISLAND SOUND

Class Demospongiae

ORDER HADROMERINA

Family Suberitidae

Suberites ficus (Johnston) Schmidt

Family Clionidae

Cliona celata Grant
Cliona lobata Hancock
Cliona vastifica Hancock
Cliona truitti Old

ORDER HALICHONDRINA

Family Halichondriidae

Halichondria bowerbanki Burton

ORDER POECILOSCLERINA

Family Desmacidonidae

Isodictya deichmannae (de Laubenfels) new comb.

Family Microcionidae

Microciona prolifera (Ellis and Solander) Verrill

Family Myxillidae

Lissodendoryx isodictyalis (Carter) Topsent

ORDER HAPLOSCLERINA

Family Haliclonidae

Haliclona oculata (Pallas) Grant
Haliclona loosanoffi sp. nov.
Haliclona canaliculata sp. nov.

ORDER DENDROCERATIDA

Family Halisarcidae

Halisarca sp. (description not included herein)

DESCRIPTIONS OF SPECIES

Order Hadromerina

Family Suberitidae Schmidt

Suberites ficus (Johnston, 1842) Schmidt, 1870

SYNONYMY:

? *Alcyonium ficus* Pallas, 1766, p. 356 [partim]
? *Spongia ficiformis* Poiret. Lamouroux, 1824, p. 349
? *Suberites ficus,* Nardo, 1833, p. 523 [partim?]
Halichondria virgultosa Johnston, 1842, p. 137
Halichondria suberea Johnston, 1842, p. 139
Halichondria ficus Johnston, 1842, p. 144
Halina suberea, Bowerbank, 1861, p. 235
Hymeniacidon subereum, Bowerbank, 1863, p. 1111
Hymeniacidon ficus, Bowerbank, 1864, p. 244
Hymeniacidon virgultosa,[2] Bowerbank, 1866, p. 193
Halichondria farinaria Bowerbank, 1866, p. 269
Chalina ficus, Bowerbank, 1866, p. 270 (Misprint?)
Suberites farinaria, Schmidt, 1866, p. 16
Ficulina ficus, Gray, 1867, p. 523
? *Suberites lütkeni* Schmidt, 1870, p. 47
Suberites ficus, Schmidt, 1870, p. 76
Suberites compacta Verrill, *in:* Verrill and Smith, 1873, p. 744 (Non *Alcyonium compactum* Lamarck, 1815, p. 166; *Halichondria compacta* Lieberkühn, 1859, p. 520)
Suberites montalbidus Carter, 1880, p. 256
? *Suberites montiniger* Carter, 1880, p. 256
Suberites virgultosa, Vosmaer, 1882, p. 32
Suberites suberea, Topsent, 1887, p. 150
Suberites latus Lambe, 1893, p. 71
Suberites farinarius, Hanitsch, 1894, p. 179
Suberites placenta Thiele, 1898, p. 39

DESCRIPTION: Block Island Sound specimens of *Suberites ficus* (Pl. 1, fig. 5) grow attached to dead lamellibranch shells (e.g., *Arctica islandica, Volsella modiolus,* and *Venericardia borealis*) or rocks. In many cases the sponges attach to the shells of living specimens of *Venericardia borealis* which remain alive although largely enclosed in the bases of sponge colonies reaching heights of 30 cm. or more. Müller (1914) noted a similar relationship of *ficus* with *Astarte* in the Barents Sea. In form the Block Island Sound colonies are similar to Müller's Barents Sea specimens; they grow out from the substratum to become flat, lobate colonies which reach considerably larger sizes than those reported by Müller, however. As a general rule, these colonies probably lie flat on the sea bottom, rather than grow vertically. In several cases shells have been found imbedded in the distal ends of the colonies, suggesting that the colonies were lying flat and had come in contact with shells on the sea bottom. Long, attenuated specimens such as Bowerbank (1874) figures (Pl. 35, fig. 3, as *Hymeniacidon virgultosa*) have not been found in this region, nor have the *"suberea"* types which grow around shells occupied by hermit crabs. The largest Block Island Sound specimen collected measures 36 x 16 x 3 cm. in length, width, and thickness. Typical specimens measure 28 x 9 x 2.5 cm. This sponge is very common on the fishing grounds of Block Island Sound, often filling the nets of hopeful fishermen who refer to it contemptuously as "elephant dung."

[2] It is of interest to note that in 1863 (p. 1129) Bowerbank regarded Johnston's *Halichondria virgultosa* as a synonym of *H. ficus.*

In consistency the colonies are quite compressible and elastic. In this respect they differ noticeably from colonies of *Suberites domunculus* in my possession, the latter being firm and incompressible. Topsent (1900) pointed out this difference between the two species and attributed the greater firmness of *domunculus* to the smaller diameters of the aquiferous canals. My own data fail to bear out Topsent's assertion. The canals in Block Island Sound specimens of *ficus* measure from 300 to 800μ in diameter; in specimens from Roscoff, France, they vary up to 600μ. On the other hand, the canals of a colony of *domunculus* from Banyuls-sur-mer, France, range from 1.0 to 1.8 mm. in diameter. It seems rather to be the greater abundance of canals in *ficus* which accounts for the difference in consistency. Cut surfaces of colonies of *ficus* are illustrated by Topsent (1900) and Müller (1914); of *domunculus,* by Celesia (1893), Lendenfeld (1898), and Topsent (1900). These illustrations confirm the more porous nature of the interior of *ficus* as compared with *domunculus.* The larger quantity of spongin which cements together the spicules in *domunculus* probably also adds to the firmness of the colonies.

The dermis of Block Island Sound specimens of *ficus* is quite uniformly perforated by pores which are outlined by a network of ridges made up of numerous microscleres packed together. In some specimens occasional tufts of megascleres reach the surface and reinforce the microsclere spiculation there. In specimens of *ficus* from Roscoff, microsceleres are less abundant and projecting tufts of megascleres more frequent in the dermis. Indeed, such specimens appear to be transitional from the condition in Block Island Sound specimens of *ficus* to specimens of *domunculus* from the Mediterranean, where the dermis is pierced exclusively by tufts of megascleres surrounding the dermal pores. Oscular and pore sizes for specimens of *ficus* and *domunculus* are given in Table 1.

The pores of specimens of *ficus* which I have examined are elongate and elliptical in outline, the diameters of the minor axes being about half that of the major axes. The pores of specimens of *domunculus* in my possession tend to be smaller and rounder than those of *ficus.* Lendenfeld (1898) found the reverse to be true in regard to ostial sizes of *ficus* and *domunculus.* The pore and oscular measurements probably have little significance, however, when made on preserved specimens. One to five oscules may occur per specimen in both species. Small slit-like fissures, presumably formed by amphipods, are common on the surface of some specimens of both species which I have studied (*see* Vosmaer, 1933).

The flagellated chambers in the two species are similar in shape (spherical or ellipsoidal) and dimensions (see Table 2).

Small, aspiculous gemmules are present in all specimens of both species examined by the writer. These are apparently present throughout the year, developing in contact with the substratum on which the sponge is growing. They were noted by Topsent (1900) as well.

Spicule sizes and the proportions of the several megasclere categories present in each case are given in Tables 3 and 4 (see also figs. 1 and 2).

Worthy of mention is the nature of the spicules present in the layer lining the hermit crab burrow in a colony of *domunculus* from Banyuls-sur-mer. These spicules are thicker than those in the rest of the sponge; included among them is a high proportion of strongyles and tylostyles with the distal end rounded instead of pointed (fig. 3). It is also of interest to point out that the ectosome has few oxeas and more tylostyles than the endosome in this specimen.

TABLE 1

PORE AND OSCULE SIZES OF *SUBERITES FICUS* AND *DOMUNCULUS*

SPECIES	LOCALITY AND AUTHOR	RANGE OF PORE SIZES	OSCULAR SIZES
S. ficus	Block Isl. Sound YPM #760 (Hartman)	86 x 74μ to 45 x 25μ	2.0 mm.
S. ficus	Block Isl. Sound YPM #774 (Hartman)	90 x 60μ	2.0 mm.
S. ficus	Block Isl. Sound YPM #779 (Hartman)	74 x 41μ to 57 x 33μ	closed
S. ficus	Block Isl. Sound YPM #2119 (Hartman)	111 x 41μ to 74 x 37μ	.....
S. ficus	Roscoff, France YPM #2110 (Hartman)	62 x 32μ to 45 x 33μ	1.0 to 1.6 mm.
S. ficus	Adriatic Sea (Lendenfeld, 1898)	30 to 14μ	1.0 to 1.5 mm.
S. ficus	France (Topsent, 1900)	30 to 10μ	3.0 to 20.0 mm.
S. domunculus	Naples YPM #2029 (Hartman)	57 x 45μ to 41 x 41μ	0.5 mm.
S. domunculus	Banyuls-sur-mer YPM #2030 (Hartman)	62 x 53μ to 50 x 32μ	1.5 to 3.0 mm.
S. domunculus	Adriatic Sea (Lendenfeld, 1898)	70 to 40μ	3.0 to 6.0 mm.

Spongin fibers are of regular occurrence in both species, *domunculus* and *ficus,* but are more extensively developed in the former. In a specimen from Banyuls-sur-mer continuous fibers enclosing tylostyles, and measuring up to 90μ across, run from the interior to the surface. In specimens of *ficus* from Roscoff, small patches of spongin (up to 20μ across) are found in places in the endosome surrounding clumps of megascleres. In Block Island Sound specimens of *ficus,* spongin is even rarer in occurrence.

Discussion: The tangled synonymies of *Suberites ficus* and *Suberites domunculus* have been exhaustively tabulated by Vosmaer (1933) and critically reviewed

TABLE 2

FLAGELLATED CHAMBER DIMENSIONS IN *SUBERITES*

SPECIES	LOCALITY AND AUTHOR	RANGE OF SIZES
S. ficus	Block Isl. Sound (YPM #2119, Hartman)	21 x 21μ to 25 x 21μ
S. ficus	Roscoff, France (YPM #2110, Hartman)	21 x 23μ to 25 x 29μ
S. ficus	Adriatic Sea (Lendenfeld, 1898)	23–25μ
S. ficus	France (Topsent, 1900)	25μ
S. domunculus	Banyuls-sur-mer, France (YPM #2030, Hartman)	25 x 25μ to 29 x 33μ
S. domunculus	Adriatic Sea (Lendenfeld, 1898)	25μ

by Burton (1953). Both authors conclude that the two species are synonymous. On the other hand, Lendenfeld (1898), Topsent (1900), Arndt (1935) and de Laubenfels (1949), among others, have regarded them as separate species. Since neither position is unequivocal at this time, it seems worth-while to review the evidence once again. For the sake of discussion, it will be assumed that two species are involved.

The spicules of *Suberites domunculus* (fig. 2) consist entirely of megascleres, including tylostyles, styles, oxeas, and intermediates between these. There is generally a high proportion of oxeas present; sometimes these outnumber the other categories. Microscleres are absent. In *Suberites ficus* (fig. 1), however, both megascleres and microscleres occur. The megascleres are chiefly tylostyles and styles, with some specimens containing a few oxeas, but the latter are never very abundant. In addition, there are varying numbers of centrotylote microscleres, ranging in shape from microstrongyles to microstyles and microxeas. Occasionally the central swelling is absent. In any one individual both smooth and microspined centrotylotes may occur, the proportions varying from specimen to specimen.

It is the great variation which occurs in the proportions of the several categories of megascleres and in the number of microscleres present which have led many authors to synonymize *ficus* and *domunculus*. Thus Vosmaer (1933, p. 436) states that the "presence or absence [of oxeas] has no relation to the presence or absence of centrotylote microscleres." Yet his own data belie this statement. From his table of spicule sizes (1933, pp. 455-456),[3] including data of other authors as well as his own, we learn the following:

[3] Bowerbank's *Hymeniacidon suberea*, Hanitsch's *"Suberites domuncula,"* and Lambe's *Suberites montiniger* and *concinnus* are omitted in this discussion, the first two because of the likelihood that spicule categories were overlooked, the last two because of their uncertain synonymy with either of the species in question.

TABLE 3

SPICULE MEASUREMENTS OF *SUBERITES FICUS*

LOCALITY	MEGASCLERES* (Tylostyles, styles, oxeas)	MICROSCLERES* (Microcentrostrongyles)	PERCENTAGE OF MEGASCLERE CATEGORIES		
			Tylostyles	Styles	Oxeas
Roscoff, France YPM #2119	103–*197*–287μ x 3.7–*5.1*–7.8μ	12.3–*24.2*–33.3μ x 1.2–*2.6*–3.5μ	48	31	21
Block Isl. Sound, Rhode Island YPM #779	168–*270*–381μ x 3.7–*6.5*–8.2μ	15.8–*24.5*–42.0μ x 1.9–*2.9*–3.5μ	92	8	—
Block Isl. Sound, Rhode Island YPM #774	144–*286*–402μ x 3.3–*6.6*–8.2μ	15.8–*24.9*–56.0μ x 1.8–*2.9*–3.5μ	96	4	—
Block Isl. Sound, Rhode Island YPM #760	152–*293*–365μ x 4.1–*6.6*–8.2μ	14.0–*25.3*–56.0μ x 1.6–*2.7*–3.7μ	85	15	—
Block Isl. Sound, Rhode Island YPM #2121	205–*304*–385μ x 4.9–*8.6*–11.5μ	15.8–*28.5*–54.3μ x 1.6–*3.1*–4.0μ	92	8	—
Block Isl. Sound, Rhode Island YPM #2119	185–*309*–377μ x 2.5–*6.9*–8.6μ	14.0–*21.2*–28.0μ x 2.3–*3.1*–3.5μ	76	24	—
Block Isl. Sound, Rhode Island YPM #775	209–*321*–410μ x 4.1–*5.9*–7.8μ	15.8–*27.6*–56.0μ x 1.6–*2.6*–3.3μ	65	35	—
Woods Hole, Mass. MCZ #6905	168–*302*–426μ x 3.7–*6.0*–8.2μ	16.0–*23.0*–42.0μ x 1.6–*2.7*–3.7μ	63	27	10

* Fifty spicules of each category measured.

TABLE 4

SPICULE MEASUREMENTS OF *SUBERITES DOMUNCULUS*

LOCALITY	NO. OF SPICULES MEASURED	TYLOSTYLES	STYLES	OXEAS
Naples YPM #2029B	100	119–*209*–295μ x 2.5–*3.7*–4.1μ 28%	168–*232*–303μ x 2.5–*4.0*–4.9μ 45%	98–*259*–320μ x 2.5–*4.0*–5.3μ 27%
Naples YPM #2029C	100	107–*214*–287μ x 2.5–*4.0*–5.3μ 50%	180–*238*–279μ x 2.9–*4.1*–5.3μ 26%	205–*284*–353μ x 2.5–*3.9*–6.2μ 24%
Naples YPM #2029A	100	90–*199*–324μ x 3.7–*4.6*–6.2μ 23%	115–*236*–365μ x 3.7–*4.4*–5.3μ 29%	115–*285*–390μ x 3.3–*4.3*–5.7μ 48%
Naples Osborn Zool. Lab. Colls.	50	98–*258*–398μ x 3.7–*5.6*–7.8μ 59%	22%	19%
		Categories not separated in measurements		
Banyuls-sur-mer, France YPM #2030	100	Dermis: 90–*182*–320μ x 3.3–*5.0*–7.4μ 44%	99–*217*–349μ x 4.1–*5.2*–7.8μ 50%	279–*348*–390μ x 4.1–*5.0*–7.0μ 6%
	100	Endosome: 144–*280*–332μ x 4.1–*5.6*–7.8μ 24%	144–*303*–373μ x 4.5–*5.9*–8.2μ 47%	275–*364*–418μ x 4.1–*5.5*–7.8μ 29%
	100	Spicules lining crab burrow: 221–*268*–320μ x 4.5–*7.5*–9.0μ 27%	234–*269*–303μ x 7.4–*8.2*–9.8μ 8%	271μ x 7.4μ 1%
		Other categories: Tylostyles with rounded distal ends: 144–*221*–275μ x 6.2–*8.0*–9.4μ 31% Strongyles: 148–*214*–312μ x 4.5–*7.8*–9.8μ 33%		

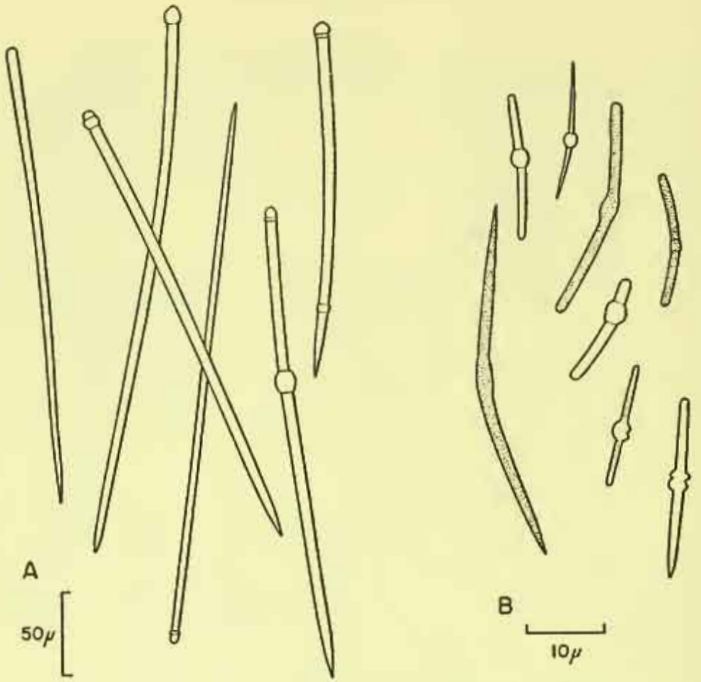


FIGURE 1. Spicules of *Suberites ficus*. A. Styles and tylostyles, some of latter with subterminal heads. B. Centrotylote microxeas, microstrongyles and microstyles. Block Island Sound. YPM #779.

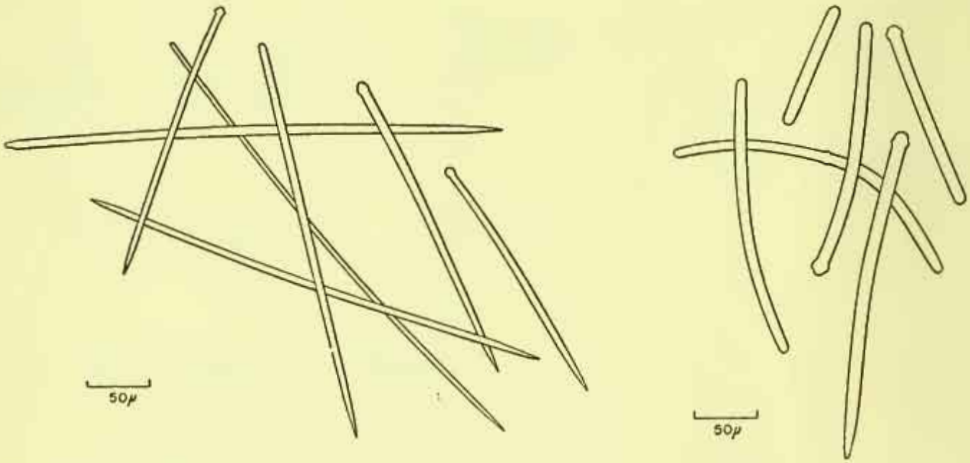


FIGURE 2. Spicules of *Suberites domunculus:* oxeas, styles, tylostyles. Banyuls-sur-mer, France. YPM #2030.

FIGURE 3. Peculiar strongyles and tylostyles of *Suberites domunculus* found in the basal layer in contact with the enclosed hermit crab. Banyuls-sur-mer, France. YPM #2030.

Specimens reported with oxeas and no microscleres—9
Specimens reported with microscleres and no oxeas—15
Specimens reported with both microscleres and oxeas—3
Specimens reported with neither microscleres nor oxeas—2

It is apparent that the oxeas and microscleres are mutually exclusive in occurrence, as a general rule. The three instances in which both microscleres and oxeas occur can be considered specimens of *S. ficus* with a few oxeas; the two cases of individuals lacking both oxeas and microscleres can be interpreted as specimens of *S. domunculus* without oxeas. Vosmaer's own records (the last eight specimens in his table) include seven specimens with oxeas varying in number from moderately frequent to numerous and with no microscleres. In the remaining specimen, microscleres are present and oxeas are described as "very rare."

Burton (1932) states that the presence or absence of microscleres is valueless as a taxonomic character for distinguishing *ficus* from *domunculus* because the microscleres in *ficus* are often scarce and hence difficult to find. However, in my experience, the simple expedient of centrifuging a suspension of spicules freed by nitric acid from a cubic centimeter of a specimen has proved a satisfactory means of finding rare categories of microscleres. It is certainly true that centrotylotes are uncommon in occasional specimens of *ficus*. It is even possible that some specimens of *ficus* lack microscleres entirely, but I know of no cases reported in the literature where proper precautions were taken to exclude the possibility that microscleres were overlooked.

It seems highly probable that northern records of *S. domunculus* reported in the literature are always misidentifications of *S. ficus*, in which the scarcity of microscleres has rendered them undetected. Several instances in which subsequent examinations of specimens of *S. ficus* have revealed the presence of microscleres which had been overlooked previously may be cited. Topsent (1900) has pointed out, for example, that Carter found centrotylote microstrongyles upon reëxamining the specimens which Johnston (1842) and Bowerbank (1866) had described as *Halichondria suberea* and *Hymeniacidon subereum*, respectively, a species lacking microscleres according to these authors. Schmidt (1870) synonymized *suberea* with *Suberites domunculus*, also having overlooked the microscleres. Hanitsch (1890), who accepted Schmidt's synonymy of *suberea* with *domunculus*, found no microscleres in specimens from the Liverpool region. Later (1891), however, he did find them in his specimens of *"suberea"* but he continued to call the species *domunculus* and to distinguish it from *ficus* without mentioning his reasons for this. Lambe (1894) pointed out that he had overlooked the microscleres in some of his specimens of *Suberites latus*, which he had described previously (1892) as a new species. De Laubenfels (1949) identified a specimen from Woods Hole as *Suberites domunculus* on the basis of the absence of microscleres, but a reëxamination of his specimen (MCZ, #6509) by the present author has revealed that microscleres are not uncommon in it. Records of *Suberites domunculus* (as defined here) from the Atlantic coast of France, Great Britain and the North Sea must all remain in doubt until the absence of microscleres has been proven by careful reëxamination.

In addition to the differences in spicule types between the two species in question, the abundant literature on these sponges reveals distinctions in form and habitat. These characters overlap in part in the two species, a fact which has augmented the confusion.

Suberites domunculus almost always grows around a gastropod shell inhabited by a hermit crab and has a massive, rounded form. Occasionally this species grows on the backs of dromiid crabs. *Suberites ficus* is more variable in form and habitat. Some specimens ("var. *subereus*") grow on shells occupied by hermit crabs and develop into massive, rounded colonies (Müller, 1914, e.g., found this form to be the most common one in the North Sea); others grow on shells of living or dead gastropods and lamellibranchs or on rocks and assume a figlike shape (which gives the sponge its specific name) or form elongate, flattened colonies which are sometimes lobose (Müller, 1914, found the latter shape common in the Barents Sea); still others ("var. *farinarius*") have an elongate, cylindrical form and grow attached to shells or rocks.

Turning now to the geographical distribution of the two species we find that *S. ficus* is a wide ranging species, having been reported from the Mediterranean area and the west coast of Africa to Senegal, from the west coast of France, the English Channel, the North Sea, the coasts of the British Isles and Norway, off Iceland and Greenland, south along the Atlantic Coast of North America to Virginia, from the Bering Sea, the Pacific Coast of North America south to Vancouver Island, and from the Pacific Coast of Asia to Japan.

S. domunculus, on the other hand, has a restricted range, overlapping that of *ficus*, in part. *S. domunculus* occurs only in the Mediterranean area, including the Black Sea, and southward along the west coast of Africa to Senegal. The *Suberites* recorded by Lendenfeld (1888) from the south and east coasts of Australia is of doubtful synonymy with *domunculus*. *Suberites heros* Schmidt (1870), from the Antilles, has been considered a synonym of *domunculus* by Topsent (1900), Vosmaer (1933), Arndt (1935), and Burton (1953), but it seems likely that Thiele (1905) is correct in regarding it as a valid species. Burton's record of *domunculus* from South Saghalin (1932) is questionable.

The information from the literature here reviewed may be interpreted in one of two ways: (1) the two species are distinct, *ficus* being a wide ranging species with *domunculus* occurring sympatrically with it over part of its range; (2) there is only one species which is polymorphic in the Mediterranean area and along the northwest coast of Africa. In my opinion, the first interpretation best fits the data reviewed.

Suberites domunculus, then, is a species which (1) has a relatively constant external form, (2) invariably occurs in association with hermit crabs or dromiid crabs, (3) lacks microscleres, (4) tends to have a high proportion of oxeas among the megascleres, and (5) has a restricted geographic range. *S. ficus*, on the other hand, (1) is a highly variable species in regard to external form and habitat, overlapping in part with *S. domunculus* in these characteristics, (2) always possesses microscleres, although the number present may vary greatly among individuals from a single population, (3) usually lacks oxeas, and (4) has an extensive geographic range.

It is hoped that this conclusion, based on previous work in the literature and a study of the limited material available to me, will be checked through a fresh attack on the problem. Some possible approaches follow: Biometric studies of large series of specimens from populations of *Suberites* in the Mediterranean, the west coast of Europe, the Arctic, and North America, would help to determine the significance of variations in spicule categories and external shape. Cytological studies, including chromosome counts, might prove useful, although the latter would be difficult because of the small size of the cells. Histochemical and bio-

chemical studies of the organic skeletal elements would be of interest. Herlant-Meewis (1949) reported the presence of spongin, elastin fibers, and cell cords in *Suberites domunculus*. Are the supplementary skeletal elements similar or different in *S. ficus*? Finally, further studies of development might reveal specific differences. Topsent (1900) described the eggs of *S. ficus;* Thomson (1887) described both eggs and sperm in the same individual of *S. domunculus* studied at the Berlin Aquarium.

The possibility exists that *ficus* itself represents a complex of species. There is a reasonable doubt as to whether *Suberites lütkeni* and *S. placenta* are synonyms of *ficus*, for example, and the populations of *ficus* occurring south of Cape Cod on the North American Coast (Verrill's *S. compacta*) may actually represent a distinct species, although further analysis is necessary to establish this.

NOTES ON RELATIONSHIPS AND NOMENCLATURE: *Suberites ficus* is often placed in the genus *Ficulina*, but this seems unwarranted in view of the close similarity of *ficus* to *domunculus*. Perhaps *Ficulina* is best considered as a subgenus of *Suberites* (as suggested by Thiele, 1905, p. 416) to receive those species having centrotylote microscleres, such as *ficus* and *lütkeni* (if the latter is indeed distinct from *ficus*).

De Laubenfels (1936, 1949) has placed *S. ficus* in the family Spirastrellidae[4] on the basis of the presence of microscleres; thus he separates *ficus* widely from the Suberitidae.[5] However, this author has placed undue emphasis on the occurrence of microscleres and has ignored the striking similarities between *ficus* and *domunculus* in general morphology. Moreover, Bergmann (1949) has demonstrated that a clear-cut difference exists in the sterols of spirastrellids and suberitids. He found clionasterol and poriferasterol in *Spheciospongia* and *Anthosigmella*, and cholestanol and neospongosterol in *Suberites domunculus* and *Suberites ficus* (the latter species is reported by him as *Suberites suberea* [from Alaska] and *S. compacta* [from Block Island Sound]). The biochemical evidence is in agreement with the morphological similarities of *S. ficus* and *S. domunculus*, and it must be concluded that the two species cannot be separated at the generic and familial levels.

If *Suberites ficus* is accepted as a species distinct from *S. domunculus*, it is a difficult matter to decide upon a valid name for it. Since authors prior to Johnston (1842) failed to mention the microscopic details necessary to separate *ficus* from *domunculus* and *carnosus*, it seems to me impossible to accept a name proposed before 1842.

Pallas (1766) is the first author after 1758 who refers to a sponge which might be *Suberites ficus*. His *Alcyonium ficus* actually includes both a sponge and a compound ascidian [*Synoicum pulmonaria* (Ellis and Solander)], as pointed out by Hartmeyer (1914). Pallas had apparently not seen a specimen ("*mihi nunquam visum*") of either the British sea-fig (an ascidian) or the Mediterranean sea-fig (a

[4] De Laubenfels (1936, 1949) named the family "Choanitidae" because Mantell (1822) had established *Alcyonium ficus* Linné as the type of *Choanites*, a genus of fossil sponges which have no apparent relationship to the recent sponge, *Suberites ficus*. Topsent (1933) and Burton (1953) have accepted the view of Lamouroux (1824) that Linné's *Alcyonium ficus* is an ascidian, and de Laubenfels (1955) has now dropped the name *Choanites* without giving a generic assignment to the species *ficus*.

[5] Burton (1953) states that de Laubenfels (1949) "appears to accept the identity of *Ficulina ficus* with *Suberites domuncula*," but in reality de Laubenfels places the two species in different families in the paper under consideration.

sponge), and was misled by the similarity of the figures of these animals given by earlier authors. He cites Imperato (1599) who figures a sponge called *Alcyonium tuberosum forma ficus;* Bauhino and Cherlero (1651) who give a copy of Imperato's figure; Mercati (1717) who describes what may be *Suberites ficus,* naming it *Alcyonium quintam antiquorum*[6]; Ray (1724) who does not refer to a sponge; Marsilli (1725) who figures a sponge which may have been *Suberites ficus,* but looks more nearly like *Petrosia ficiformis* (Poiret); and Ellis (1755) who clearly has reference to the ascidian. It is entirely possible that some of Pallas' indications do indeed refer to *Suberites ficus,* but there is no way of being certain of this since the figlike form shown in the figures of all of these authors is assumed occasionally by *Suberites carnosus* and possibly also by *domunculus.* Pallas' name is thus without significance today. The same is true of Linné's (1767) name *Alcyonium ficus;* this author simply cites a few of the same authors mentioned above, namely, Bauhino and Cherlero, Ray, Marsilli, Ellis, and Pallas. Linné's use of *ficus* also includes both an ascidian and a sponge, the latter undeterminable. Battarra (1773) cites Imperato's *Alcyonium tuberosum Ficus forma* (*sic*) without description or figure; Ellis and Solander (1786) figure a sponge called "the sea-fig" which they clearly differentiate from the compound ascidian, but they do not give a scientific name for it. Hartmeyer (1914) lists other references to *Alcyonium ficus* which are either undeterminable or include both an ascidian and a sponge.

Poiret (1789) mentions an *Alcyonium ficus* which is certainly a sponge (it is described from the Mediterranean region which is outside the range of the ascidian; Poiret also mentions the presence of an oscule); although this is probably a *Suberites* [he calls it "the fig-shaped sea cork," thus anticipating the name *Suberites* which was first used by Nardo (1833)], it is not possible to say with certainty to which species it belongs. Poiret differentiates *Alcyonium ficus* from another sponge, similar in external shape, which he calls *Spongia ficiformis.* This species, now called *Petrosia ficiformis* (Poiret), adds further confusion to the literature, although Nardo (1844) had recognized Lamarck's citation of this species as distinct from *Suberites ficus* and had named it *Reniera dura* var. *ficiformis.* Burton (1953) has tabulated Topsent's (1933) views on the early nomenclatural history of this species. Topsent points out that although Poiret's *Spongia ficiformis,* and most subsequent references to it, actually refer to *Petrosia ficiformis,* the citation of this species given by Lamouroux (1824) probably refers to *Suberites ficus,* the name of which should be changed to *ficiformis.* But once again Lamouroux's description is open to confusion with other species of *Suberites,* and this name cannot be accepted for *Suberites ficus* in my opinion.

Burton accepts Topsent's view that "all references to the so-called *Ficulina ficus* prior to Lamouroux (1824) are concerned with either *Petrosia ficiformis* Poiret or an ascidian." He thereby rejects the conclusions of Hartmeyer, who, in my opinion, has given a sounder review of the early literature. There is little doubt in my mind that some of the authors prior to Lamouroux did indeed have reference to a sponge other than *Petrosia ficiformis,* and this sponge was most probably a *Suberites.* But I do not feel that any of these authors has given a description which enables *ficus* to be distinguished from other members of the genus.

[6] Mercati gives three figures of this animal. Two have the figlike form portrayed earlier by Imperato (1599), but only one of these is shown with a large central oscule and may represent a *Suberites.* The third animal figured is lobate and lacks distinct oscules.

Nardo (1833) established the genus *Suberites* to include the following species: "*Suberites typus* N., *Alc. domuncula* Olivi, *S. ficus* N., *Sp. ficus?* auct., *S. volubilis* N." The first and last mentioned species are *nomina nuda,* no description being given in the paper mentioned or in any of his subsequent works. (It is possible that these species are described in his posthumous publications (1847) which I have not seen.) It is of interest to note that Nardo questioned the synonymy of his *Suberites ficus* with *Spongia ficus* auct. In 1844 Nardo clarified his concept of *Suberites* (which he now spelled *Suburites) ficus,* describing it as a synonym of *Alcyonium ficus* Olivi and Ginnani's (1757) *Alcyonio minore in forma di fico frutto.* Although Nardo described the megascleres of this species, he did not mention the diagnostic microscleres.

If the presence of microscleres is accepted as a valid character for distinguishing *ficus* from *domunculus,* then the type chosen should make reference to their presence. So far as I have been able to determine from the literature, Johnston's (1842) descriptions of *Halichondria virgultosa, H. suberea,* and *H. ficus* are the first unequivocal references to the sponge in question. Johnston does not mention the presence of microscleres in any of these species, but their occurrence has been affirmed in all by subsequent authors who reëxamined Johnston's material. The name *virgultosa*[7] has page priority (p. 137); the presence of microscleres in Johnston's specimen was confirmed by Bowerbank (1866, pp. 193–195).[8] The species *suberea* is mentioned next (p. 139); the presence of microscleres in Johnston's specimen was confirmed by Carter (Hanitsch, 1891, p. 218). The name *ficus* is listed last of all (p. 144); Bowerbank (1864, p. 244 and Pl. IV, fig. 95) figured a microsclere from a specimen which he regarded as identical to those of Johnston. The specific name *virgultosa* has priority on the basis of strict adherence to the Rules of the International Commission on Zoological Nomenclature. However, the name *ficus* has become so well established that it seems desirable to conserve it, especially since this is the first name which was used with a figure of the diagnostic microsclere (Bowerbank, 1864). Schmidt (1870) first referred Bowerbank's *Hymeniacidon ficus* [= *Halichondria ficus* Johnston] to the genus *Suberites.*

The name *domunculus* was first used by Olivi (1792); as Burton (1953) has noted, if both *ficus* and *domunculus* are accepted as valid species, it is impossible to say which of the two species Olivi had at hand, since both may be found on shells occupied by hermit crabs. Lieberkühn (1859) was apparently the first author to describe the skeletal characteristics of *domunculus* as this species is understood in the present paper. This author uses the name *Halichondria compacta,* however, which should therefore replace *domunculus.*

Thus the names of both of these common sponges, which have become well known in the literature as *domunculus* and *ficus,* would appear to be invalid. The present writer feels that there is ample reason to conserve the commonly used names, and the question will have to be submitted to the International Commission on Zoological Nomenclature. It seems unwarranted to follow this course, however, until the present uncertainty about the distinctness of the two

[7] Johnston's citation of Lamarck's *Spongia virgultosa* is open to question. Topsent (1933) was unable to find Lamarck's specimen, which remains undeterminable.

[8] Burton (1953) maintains that Johnston's *Halichondria virgultosa* is not the same species as Bowerbank's *Hymeniacidon virgultosa,* but Bowerbank (1866) states, "The type specimen of this species, described by Dr. Johnston . . . is in the possession of Mr. Bean, of Scarborough, where I have had the pleasure of seeing it."

species is clarified. In the meantime, retention of the commonly used specific names would seem to be the best procedure to follow.

DISTRIBUTION OF *Suberites ficus* IN NORTH AMERICA: Atlantic Coast of North America, Hudson Bay to Virginia; Canadian Arctic; Pacific Coast of North America, Bering Sea to Vancouver Island.

Vancouver Island and mainland of British Columbia, 12 to 45 meters (as *S. latus,* Lambe, 1892, p. 72); Bering Sea and North Pacific Ocean (as *S. suberea,* Lambe, 1894, p. 127; 1900a, p. 161); Unalaska Island (as *S. montalbidus,* Lambe, 1894, p. 128); Bernard Harbor and Stapylton Bay, North West Territory, 6 to 28 meters (as *Ficulina ficus,* Dendy and Frederick, 1924, p. 6); Hudson Bay, 35 to 55 meters (as *S. montalbidus,* Lambe, 1900b, p. 24); Gulf of St. Lawrence (*fide* Procter, 1933, p. 108); Sable Island, N.S. (Lambe, 1896, p. 193); Mt. Desert Island Region, Maine, 52 meters (as *S. montalibidus,* Procter, 1933, p. 108); Cape Cod, Mass., 28 meters (as *S. compactus,* Verrill, 1880, p. 232); off Martha's Vineyard, Mass., 18 meters (as *S. compactus,* Verrill, *in*: Verrill and Smith, 1873, p. 744); Nantucket (as *S. compactus,* Verrill, *ibid.,* and 1880, p. 232; Sumner, Osburn, and Cole, 1913, p. 558); Woods Hole, Mass. (as *Choanites ficus* and *Suberites domunculus,* de Laubenfels, 1949, pp. 19, 20); Block Island Sound, 20 to 40 meters (Hartman); eastern shore of Virginia (as *S. compactus,* Verrill, *in*: Verrill and Smith, 1873, p. 744).

FAMILY CLIONIDAE Gray

Cliona celata Grant, 1826b

SYNONYMY: *See* Topsent (1900, pp. 32-34) and Vosmaer (1933, pp. 349-383). As usual Vosmaer has obscured relationships within the Clionidae by excessive lumping. Such species as *Cliona lobata* Hancock, *Cliona viridis* (Schmidt) Fischer, and *Cliona schmidti* (Ridley) Topsent are unquestionably valid species although Vosmaer regards them as synonyms of *Cliona celata. Cliona caribboea* Carter may be a synonym of *celata* (*see* de Laubenfels, 1936, p. 155), although its pattern of growth in the γ-stage is certainly different from that of *celata.*

DISCUSSION: *Cliona celata* is a very abundant sponge in Long Island Sound where it is considered a pest by oyster farmers. All three stages named by Vosmaer (α-, β-, and γ-stages) are found, the α-stage, (Pl. 1, figs. 1, 2) being most common, living in galleries which it excavates in the shells of oysters and other molluscs (*see* Part II). The β-stage (Pl. 1, fig. 3) is a transitory one passed through as the sponge overgrows the calcareous substratum on which it first settles. The free-living γ-stage (Pl. 1, fig. 4) is especially common on abandoned, undisturbed oyster beds, as would be expected, and it is not infrequently found at mean low water level growing on rocks. Intertidal colonies remain alive and active through the winter. The γ-stage colonies usually have no trace of the original calcareous substratum remaining, the sponge having completely destroyed it. Leidy (1890) states that New Jersey fishermen call the γ-stage colonies "bay pumpkins." Long Island Sound oystermen refer to the free-living colonies as "porpoise dung."

In life, the γ-stage colonies are golden yellow in color (Maerz and Paul, 1950, Pl. 10, H-5, K-5, L-6) externally, the tubules being somewhat darker when contracted. The endosome varies from deep chrome (*op. cit.,* Pl. 9, L-7) to hazel (*op. cit.,* Pl. 13, L-8).

The shell perforations through which the incurrent papillae protrude vary from 0.8 to 2.5 mm. in diameter; those through which oscular papillae protrude are 2.0 to 4.5 mm. in diameter.

The general morphology of *Cliona celata* has been well described by Topsent (1900), Vosmaer (1933; this work must be read critically, however, because of Vosmaer's broad concept of *C. celata),* and Volz (1939).

European authors (Topsent, 1900, and Vosmaer, 1933) have recorded the presence of spirasters in young colonies of *C. celata,* and Hopkins (1956a) reports these spicules in some specimens of this species from Louisiana. Microscleres have not been found in New England specimens of *C. celata* regardless of age. Similarly, the oxeas reported by Topsent and Vosmaer (*loc. cit.)* in occasional colonies of *C. celata* have not been found in American specimens, including the Gulf Coast populations studied by Hopkins. Table 5 compares spicule sizes of *C. celata* from Long Island Sound with those reported from other localities on the American Atlantic Coast.

Eggs observed in Long Island Sound specimens of *Cliona celata* are spherical, varying from 32 to 38μ in diameter. The nucleus varies from 14 to 16μ in diameter; the nucleolus is 5μ. Topsent (1911) reports that the eggs of European specimens measure 45μ.

DISTRIBUTION IN NORTH AMERICA: Gulf of St. Lawrence to South Carolina; Gulf Coast of Louisiana and Texas; Pacific Coast of North America.

Gulf of St. Lawrence (Lambe, 1900b, p. 164); Prince Edward Island (Lambe, 1896, p. 202; Old, 1941, p. 12); Mount Desert Island, Maine (Procter, 1933, p. 114); Casco Bay, Maine (Kingsley, 1901, p. 161, as *Cliona sulphurea);* Portland Harbor, Maine (Verrill *in*: Verrill and Smith, 1873, p. 744); Vineyard Sound, Mass., 11-18.5 meters (Desor, 1851, p. 68, as *Spongia sulphurea*); Vineyard Sound, Mass., 2 to 30 meters (Verrill, 1871, p. 359, as *Spongia sulphurea* Desor; Verrill *in*: Verrill and Smith, 1873, p. 744 and 1880, p. 232, as *Cliona sulphurea);* Vineyard Sound and Buzzards Bay, Mass., 4 to 35 meters (Sumner *et al.,* 1913, p. 557); Woods Hole, Mass. (Allee, 1923, p. 175; de Laubenfels, 1949, p. 23); Block Island Sound, R. I., 20 to 40 meters (Hartman); off Long Island (Verrill, 1878, p. 406, as *Cliona sulphurea);* Long Island Sound, low water to 28 meters (Verrill *in*: Verrill and Smith, 1873, p. 744; Old, 1941, p. 12; Hartman); Great Egg Harbor, N. J. (Verrill *in*: Verrill and Smith, 1873, p. 744, as *Cliona sulphurea);* Great Egg Harbor and Little Egg Harbor, N. J. (Leidy, 1857, pp. 162-163; 1890, p. 70; Topsent, 1887, p. 9); Delaware Bay (Old, 1941, p. 12); Ocean City and Sinnepuxent Bay, Maryland (Old, 1941, p. 12); Chincoteague Bay, Virginia (Old, 1941, p. 13); Chesapeake Bay (Old, 1941, pp. 12-13); Ft. Macon, N. C. (Coues and Yarrow, 1879, p. 312); Beaufort Harbor, N. C. (George and Wilson, 1919, p. 138; McDougall, 1943, p. 331; de Laubenfels, 1947, p. 34); South Carolina (Lunz, 1935, p. 2; Hopkins, 1956b, p. 20); St. George's Sound, Florida (Menzel, 1956, p. 1); west coast of Florida (Carter, 1885, p. 207: = *C. caribboea*?); Louisiana (Moore, 1899, p. 93; Cary, 1906a, p. 21; 1906b, p. 50; 1907a, p. 28; 1907b, p. 52; all as *Cliona sulphurea;* Hopkins 1956a, p. 49); Aransas Bay, Texas, 1½ meters (Hartman; also unverified records by Hopkins, 1956a, p. 54); California (de Laubenfels, 1932b, p. 47; Hartman, *in*: Smith *et al.,* 1954, p. 19).

TABLE 5

SPICULE DIMENSIONS OF *CLIONA CELATA*

LOCALITY	AUTHOR	GROWTH STAGE	RANGE OR RANGE AND MEAN OF LENGTH X WIDTH*—TYLOSTYLES
Prince Edward Island	Lambe, 1896	α	229–320μ x 4.9μ
Mt. Desert Island, Me.	Procter, 1933	α	243–*324*–364μ (mode) Heads usually subterminal
Woods Hole, Mass.	de Laubenfels, 1949	α	300μ x 10μ
Long Island Sound and Chesapeake By	Old, 1941	α	220–400μ x 4–10μ
Off Momauguin, East Haven, Conn. YPM #767	Hartman	α	193–*286*–369μ x 4.1–*7.1*–10.3μ
New Haven Harbor, Connecticut YPM #835	Hartman	α	189–*274*–357μ x 4.1–*6.2*–8.2μ
New Haven Harbor, Connecticut YPM #813	Hartman	α	172–*288*–332μ x 5.3–*7.6*–10.7μ
Off Stratford Pt., Connecticut YPM #766	Hartman	α	176–*307*–414μ x 4.1–*7.2*–9.4μ
Off Momauguin, East Haven, Conn. YPM #767	Hartman	β	213–*296*–385μ x 4.1–*8.4*–11.1μ
Off Momauguin, East Haven, Conn. YPM #767	Hartman	γ	213–*323*–377μ x 7.0–*9.1*–11.9μ
Beaufort Harbor, North Carolina	George and Wilson, 1919	α	200–400μ x 4–9μ
Beaufort County, South Carolina YPM #1859	Hartman	α	238–*350*–426μ x 8.2–*12.5*–17.2μ
Parris Island, South Carolina YPM #1860	Hartman	α	221–*306*–398μ x 7.0–*9.5*–12.3μ
California	de Laubenfels, 1932b	α	200–270μ x 2–9μ

* Measurements reported by Hartman are based on 50 spicules per specimen.

Cliona lobata Hancock, 1849

SYNONYMY: *See* Topsent (1900, pp. 70-71) and Vosmaer (1933, pp. 362-364).

DISCUSSION: *Cliona lobata* is another common boring sponge on the oyster beds of Long Island Sound. The shell perforations produced by *C. lobata* are slightly larger (incurrent, 0.2 to 0.5 mm.; excurrent, 0.8 to 1.6 mm.) than those made by *C. vastifica,* but these two species are easily confused in the field. *Cliona lobata* sometimes produces perforations in a reticulate pattern. The color of the colonies is pale yellow.

The morphology of this sponge has been described by Topsent (1900) and Volz (1939). The spicules (fig. 4) are (1) tylostyles which may have subterminal or multiple heads and (2) spirasters of two categories—(a) those with spines arranged in a spiral pattern around the spicule, the spines being more prominent at the angles and ends of the spicule and (b) those with more abundant spines distributed at random over the surface. Spicules of the latter category are generally smaller in size than the former. Topsent (1900) has figured the two types of spirasters.

Vosmaer (1933) pointed out the similarity of colonies of *Cliona lobata* to young spiraster-containing colonies of *Cliona celata* found in European waters,

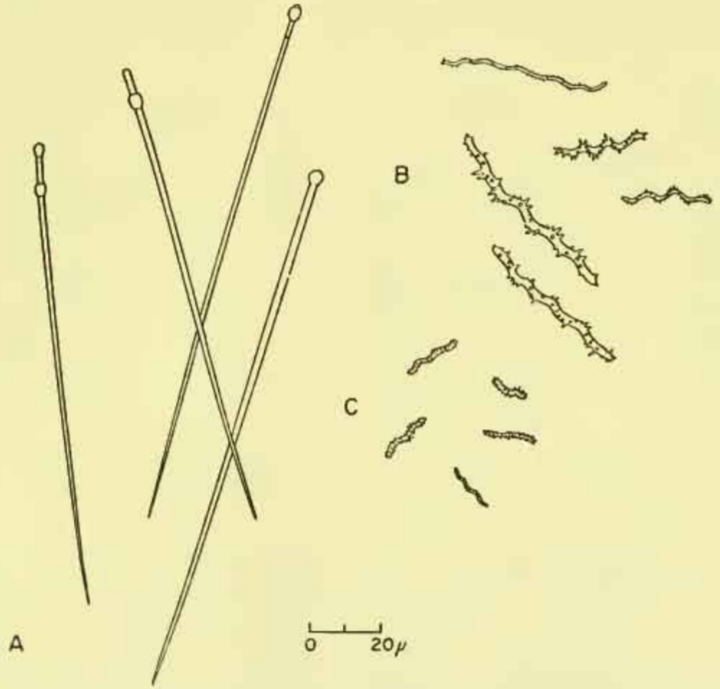


FIGURE 4. Spicules of *Cliona lobata.* A. Tylostyles. B. Spirasters with spines in spiral pattern. C. Spirasters with spines more evenly distributed. New Haven Harbor, Conn. YPM #1852L.

and inquired if "we are simply dealing with small, enfeebled specimens of *C. celata.*" He relegated *lobata* to synonymy with *celata.* Topsent (1900), on the other hand, had emphasized two differences between the two species: (1) *C. lobata*

TABLE 6

SPICULE DIMENSIONS OF *CLIONA LOBATA*

LOCALITY	RANGE OR RANGE AND MEAN OF LENGTH X WIDTH		
	TYLOSTYLES*	SPIRASTERS*	
		Spines arranged in spiral pattern	Spines evenly distributed
New Haven Harbor, Connecticut YPM #813	156–*198*–234μ x 2.5–*3.5* –4.1μ	26–43μ x 2.6–5.3μ (8%)	7.9–*17.1*–24.5μ x 1.8–*2.7*–3.9μ (92%)
New Haven Harbor, Connecticut YPM #1852A	172–*197*–226μ x 2.1–*3.1*–4.1μ	26–39μ x 3.5μ (6%)	7.0–*17.1*–26.3μ x 1.8–*2.3*–3.5μ (94%)
New Haven Harbor, Connecticut YPM #1852C	168–*208*–250μ x 1.6–*2.8*–4.1μ	26–50μ x 3.7–4.4μ (16%)	14.0–*18.0*–21.0μ x 1.8–*2.5*–3.7μ (84%)
New Haven Harbor, Connecticut YPM #1852D	152–*191*–217μ x 1.2–*2.4*–3.7μ	37–39μ x 3.9–5.3μ (6%)	10.5–*18.6*–24.5μ x 1.6–*2.7*–3.9μ (94%)
New Haven Harbor, Connecticut YPM #1852E	168–*195*–230μ x 2.1–*3.4*–4.1μ	30–35μ x 3.5–4.4μ (6%)	10.0–*17.0*–21.0μ x 0.9–*2.5*–3.9μ (94%)
New Haven Harbor, Connecticut YPM #1852L	148–*180*–209μ x 1.2–*2.0*–2.9μ	28–44μ x 3.5–5.3μ (12%)	14.0–*19.0*–26.0μ x 1.4–*2.5*–3.5μ (88%)
Chesapeake Bay (Old, 1941)	150–250μ x 3–4μ	15–50μ x 2μ	

* All measurements (except those of Old) based on 50 spicules of each category per specimen.

has smaller papillae protruding from smaller perforations, and (2) it has a high frequency of trilobed tylostyles. Vosmaer (1933) discounted the importance of the latter character because such variant types of tylostyles are also found in other clionids. In American waters, *Cliona lobata* is readily distinguishable from *C. celata,* however. The papillae and shell perforations of the former show no overlap in size with those of the latter; *C. lobata* always has an abundance of spirasters, while *C. celata* always lacks these spicules, in New England waters at least.

Distribution in North America: Long Island Sound to South Carolina; Louisiana; Texas (?); California.

New Haven Harbor and vicinity, Conn., 20 meters (Hartman); Cold Spring Harbor, Great South Bay, Long Island, N. Y. (Old, 1941, p. 13); Chesapeake Bay

(Old, 1941, p. 13); Chincoteague Bay, Virginia (Old, 1941, p. 13); Beaufort Harbor, N. C. (Old, 1941, p. 13); Beaufort Co., S. C. (Hartman, specimen received from Mr. Nathan Bowman); South Carolina (Hopkins, 1956b, p. 20); Louisiana (Hopkins, 1956a, p. 49); Texas (unverified record by Hopkins, 1956a, p. 54); California (Hartman, *in*: Smith *et al.*, 1954, p. 19).

Cliona vastifica Hancock, 1849

SYNONYMY: *See* Lendenfeld (1898, p. 86, under the name *Vioa vastifica*); Topsent (1900, pp. 56-57); and Vosmaer (1933, pp. 402-411).

DISCUSSION: This species of boring sponge is found commonly on oyster beds in Long Island Sound, occurring from mean low water to depths of at least 10 meters. It is less common than *C. celata* and never, to my knowledge, overgrows its substratum completely to form free-living colonies as is true of *celata*.

The morphology of *Cliona vastifica* has been described by Nasonov (1883, as *Cliona stationis*); Lendenfeld (1898); Topsent (1900); Vosmaer (1933); and Volz (1939). The spicules (fig. 5) are tylostyles which sometimes have subterminal or multiple heads; acanthoxeas, which are often more abundant than the tylostyles; and spirasters. The oxeas are usually spined but occasionally smooth or spined

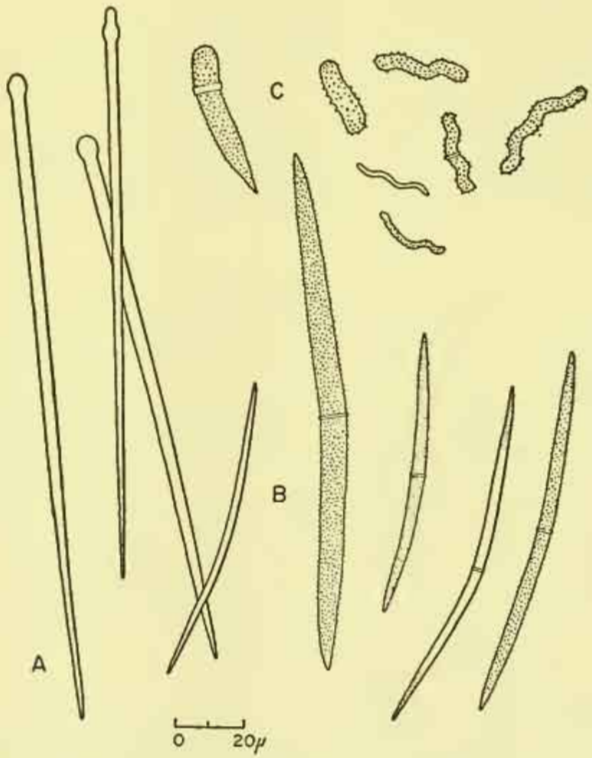


FIGURE 5. Spicules of *Cliona vastifica*. A. Tylostyles. B. Smooth and microspined oxeas. C. Smooth and microspined spirasters. (To left of C is a microspined style.) New Haven Harbor, Conn. YPM #834.

only at the ends. In Long Island Sound specimens, the oxeas generally have a slight central swelling; a few lack this characteristic. In specimens from the Bay of Fundy examined by the writer a large percentage of the oxeas likewise show traces of a central swelling; on the other hand, in specimens from South Carolina (received from Mr. Nathan Bowman) only about 30 per cent of the oxeas exhibit central swellings. Topsent (1900) figures several acanthoxeas with marked central swellings from French specimens of *vastifica,* but other European authors have not reported them.

New England colonies of *C. vastifica* are light yellow in color when alive. The shell perforations through which the incurrent papillae protrude vary from 0.2 to 0.4 mm. in diameter; those through which the excurrent papillae protrude vary from 0.6 to 1.4 mm. in diameter. The shell perforations of colonies living in thin shells (such as *Pecten magellanicus*) are often arranged in reticulate patterns; this is seldom the case in oyster shells, where the perforations are spaced at random.

Table 7 compares spicule measurements of Long Island Sound specimens with those from other localities on the North American Coast.

DISTRIBUTION IN NORTH AMERICA: From the Bay of Fundy to South Carolina; Gulf of Mexico—northwest coast of Florida, coasts of Louisiana and Texas (?), and Gulf of Campeche, Mexico.

Off Grand Manan Island, N.B. (Hartman); Fipennies Ledge, Gulf of Maine, 70 meters (Hartman); Stellwagen Bank, Massachusetts Bay, 40 meters (Hartman); Block Island Sound, 20–40 meters (Hartman); Long Island Sound, mean low water to 10 meters (Hartman; Old, 1941, p. 13); York River, Chesapeake Bay (Old, 1941, p. 13); Beaufort Harbor, N. C. (Old, 1941, p. 13); South Carolina (Lunz, 1935, p. 2; Hopkins, 1956b, p. 20); Apalachicola Bay, Florida (Pearse and Wharton, 1938, p. 635); Louisiana (Hopkins, 1956a, p. 49); Texas (unverified report by Hopkins, 1956a, p. 54); Campeche Bank, Mexico (Topsent, 1889, p. 35).

Cliona truitti Old, 1941

DISCUSSION: This species has not been found by the present writer along the Connecticut shores of Long Island Sound, although Old (1941) reports it from the north shore of Long Island, New York. It is a brackish water form differentiated from *vastifica* in regard to the sizes and shapes of oxeas and spirasters. The oxeas are somewhat longer than those of *vastifica* and almost always have a central swelling which is frequently pronounced and may be multiple. As has been pointed out previously, however, traces of a central swelling are characteristic of most of the oxeas of *C. vastifica* in specimens from the New Haven region and the Bay of Fundy. Topsent (1900) has figured oxeas from French specimens of *vastifica* in which the central swellings are as well developed as those in *C. truitti.* The microspines on the oxeas of *truitti* are smaller, and the percentage of smooth oxeas is higher than in *vastifica.* The spirasters of *C. truitti* are considerably smaller and less contorted than those of *vastifica.*

It is possible that the brackish water populations which Old has named *truitti* are simply ecophenotypes of *vastifica,* a thesis supported by the occurrence of similar variants in brackish waters in other parts of the world (see Part III). On the other hand, Old's distribution data give no indication of gradual variation with decreasing salinity; the boundary between the ranges of the two species is very sharp, especially in Chesapeake Bay (fig. 44), with no zone of overlap. An

TABLE 7

SPICULE DIMENSIONS OF *CLIONA VASTIFICA* AND *CLIONA TRUITTI*

LOCALITY	AUTHOR	RANGE OR RANGE AND MEAN OF LENGTH X WIDTH		
		Tylostyles*	Oxeas**	Spirasters*
Cliona vastifica: Grand Manan Isl., N.B. YPM #893	Hartman	164–*223*–295μ x 3.7–*4.9*–7.4μ	62–*93*–131μ x 2.1–*3.8*–6.2μ	9.0–*13.7*–20.3μ x 1.7–*2.4*–3.8μ
New Haven Harbor, Conn. YPM #834	Hartman	139–*202*–250μ x 2.9–*4.0*–5.7μ	70–*114*–164μ x 2.9–*5.2*–8.6μ	9.0–*13.1*–18.8μ x 0.9–*2.2*–3.0μ
New Haven Harbor, Conn. YPM #1851A	Hartman	144–*201*–234μ x 2.1–*3.4*–4.5μ	57–*108*–148μ x 2.1–*4.3*–6.2μ	7.5–*12.1*–16.5μ x 1.5–*2.2*–3.8μ
New Haven Harbor, Conn. YPM #1851B	Hartman	176–*220*–279μ x 2.5–*3.8*–4.9μ	57–*100*–156μ x 2.1–*4.2*–7.8μ	9.0–*13.0*–16.5μ x 1.7–*2.3*–3.0μ
Chesapeake Bay	Old, 1941	160–250μ x 3–5μ	50–110μ x 2.5–4.0μ	6–23μ x 1.0–3.5μ
Georgetown Co., S. C. YPM #1855	Hartman	168–*207*–246μ x 2.1–*4.1*–5.7μ	62–*100*–135μ x 2.1–*3.8*–5.3μ	9.0–*12.3*–18.0μ x 1.4–*1.8*–2.7μ
Beaufort Co., S. C. YPM #1856	Hartman	180–*213*–258μ x 3.7–*4.6*–7.0μ	82–*117*–160μ x 2.9–*4.1*–5.3μ	9.0–*12.2*–17.3μ x 1.5–*2.3*–3.2μ
Cliona truitti: Chesapeake Bay (?)	Old, 1941	190–225μ x 2.5–3.5μ	110–130μ x 4–5μ	7–12μ x 0.5–2.0μ
Charlestown Co., S. C. YPM #1854	Hartman	160–*206*–262μ x 3.3–*4.3*–5.7μ	90–*127*–168μ x 2.9–*4.0*–5.3μ	6.0–*10.4*–15.0μ x 1.5–*2.2*–3.2μ

* Measurements reported by Hartman based on 50 spicules per specimen.
** Measurements reported by Hartman based on 100 spicules per specimen.

investigation of this matter through transplantation experiments would be of interest. Hopkins (1956a, 1956b) reports an overlap in the ranges of *Cliona vastifica* and *C. truitti* in Louisiana and South Carolina, however, virtually ruling out this hypothesis. It is of interest to note, nevertheless, that in South Carolina Hopkins (1956b) reports intermediates between *Cliona vastifica* and *C. spirilla,* another brackish water species.

In the only specimen of this species available to me (from South Carolina), the shell perforations made by the incurrent papillae vary from 0.1 to 0.3 mm. in diameter; those made by the oscular papillae vary from 0.4 to 0.6 mm.

DISTRIBUTION IN NORTH AMERICA: Long Island Sound to South Carolina; Louisiana; Texas (?).

Long Island Sound (Old, 1941, p. 13); Chesapeake Bay (Old, 1941, p. 13); Choptank River, Patuxent River, Potomac River, St. Mary's River, Wicomico River, Sinnepuxent Bay, Maryland (Old, 1941, p. 13); Rantowles Creek, Charleston County, S. C. (Hartman, specimen received from Mr. Nathan Bowman); South Carolina (Hopkins, 1956b, p. 20); Louisiana (Hopkins, 1956a, p. 49); Texas (unverified record by Hopkins, 1956a, p. 54).

ORDER HALICHONDRINA
FAMILY HALICHONDRIIDAE Gray
Halichondria bowerbanki Burton, 1930b

SYNONYMY:

Halichondria coalita, Johnston, 1842, p. 135, Pl. XII, fig. 1.

Halichondria coalita, Bowerbank, 1866, p. 238; 1874, p. 102, Pl. XLI, figs. 18–20.

Halichondria bowerbanki Burton, 1930b, p. 489. See this paper for further details.

SHAPE AND SIZE OF COLONIES: Young colonies form thin encrustations (Pl. 4, figs. 4, 5) on rocks and algae. Colonies growing on the undersides of rocks retain an encrusting form, the oscules not at all or only slightly raised above the general surface of the colonies. Colonies growing in more exposed situations soon develop vertical outgrowths which may be low tubules bearing terminal oscules or lamellate ridges with oscula at their summits. Older colonies are variable in shape but can be reduced to three general types: (1) colonies consisting of masses of anastomosing branches, the branches sometimes being very thin (1–3 mm.; Pl. 4, figs. 6, 7, 8) but usually thicker (up to 6–8 mm.; Pl. 4, fig. 1). The largest colony of this type in my collections measures 8 cm. high and 8 x 5 cm. across. (2) Colonies with a massive base from which arise vertical branches, more or less rounded in cross section, irregularly placed (Pl. 3, figs. 7, 8 and Pl. 4, fig. 3), sometimes branching again or anastomosing with neighboring branches (Pl. 3, figs. 4, 5). The largest colony of this type in my collections measures 7 cm. high and spreads out 16 cm. in one direction, 9 cm. in the other. (3) Colonies with a massive base from which arise lamellate ridges, the distal edges of which grow out into flattened processes (Pl. 3, figs. 6, 9 through 12). Largest colony collected: 6 cm. high and 9 x 9 cm. across. In some cases the lamellate processes grow up from the base of the colony in a circular pattern to form "chimneys" (Pl. 4, fig. 2) showing some resemblance to colonies of *H. panicea* figured by Bowerbank (1874, p. 39, figs. 1, 2). In some colonies both flattened and rounded branches are found (Pl. 3, figs. 1, 2, 3).

Individuals studied at the Plymouth Laboratory, England, and the Station Zoologique, Sète, France, fall into the second category listed above. Most of the colonies collected in Europe have a massive base from which rounded, vertical branches arise. One colony dredged off Plymouth, England, is made up of numerous anastomosing branches.

COLOR IN LIFE: Colonies of this species vary considerably in color. In sum-

mer, the colonies are various shades of orange brown, cinnamon, topaz, yellow beige, hazel, and bronze. (Maerz and Paul, 1950, Pl. 12, F-7, G-5, J-7, J-8, L-8; Pl. 13, F-6, G-6, J-7, J-8, J-9; Pl. 14, I-9). Colonies containing zoochlorellae are olive green (Maerz and Paul, 1950, Pl. 15, J-2). Winter specimens are darker in hue, varying from cinnamon to drab, or in the case of specimens with zoochlorellae, to olive drab and olive brown (Maerz and Paul, 1950, Pl. 12, F-7, H-7; Pl. 13, D-4, F-4; Pl. 14, E-4, E-5, H-3; Pl. 15, H-5, J-7). Some colonies degenerate in part during the winter, losing their flagellated chambers, and becoming lighter in color. Such colonies are apricot, buff, or cinnamon in color (Pl. 10, I-7, J-7; Pl. 11, G-7, G-8; Pl. 12, F-9, G-7, H-7).

Specimens examined at Plymouth, England, tended to be dark beige to light cinnamon in color (Maerz and Paul, 1950, Pl. 10, D-3, F-4, F-5; Pl. 11, D-4, E-5; Pl. 12, D-6). The tips of the branches tended to be somewhat lighter (often near Pl. 10, D-2).

Consistency: Moderately firm and compressible.

Surface: The surface of colonies of this species is irregular, being raised into low mounds and ridges. In some specimens occasional spicule tracts pierce the surface slightly, raising the dermis into low conules. This is usually not the case, however.

Oscules: The oscules of *Halichondria bowerbanki* are highly variable in size and position. They are sometimes borne on the summits of branches, but are also distributed along the sides of branches and over the general surface of the colony. Not all vertical branches bear terminal oscules. The oscules are elliptical or circular in outline, the dimensions of the axes varying from 135 x 100μ to 5.0 x 2.5 mm. The majority vary from 1.0 to 2.5 mm. in diameter. Any one colony may have oscules of widely different sizes. Although most of the oscular measurements were made on preserved specimens, a similar range of sizes was observed in living specimens examined.

Burton (1930b) states that the oscules of *H. bowerbanki* are inconspicuous, perhaps because they were closed in the specimens examined by him. Although I was unable to study Burton's type specimen, all individuals which I collected at Plymouth, England, and Sète, France, have the same range of oscular size and position as those described above from the American populations.

Pores: The pores, elliptical to circular in outline, show some tendency toward forming vaguely defined groups on the surface. Pore size variation in three specimens follows:

YPM #847. Pine Orchard, Conn. 33 x 33μ to 20 x 20μ (mean of 7, 29 x 25μ)

YPM #849. Hammonasset, Conn. 54 x 41μ to 16 x 16μ (mean of 50, 31 x 24μ)

YPM #860. Double Beach, Conn. 68 x 43μ to 13 x 9μ (mean of 50, 36 x 21μ)

Ectosomal anatomy: The dermal membrane is made up of a layer of thin exopinacocytes. In thin sections perpendicular to the surface of the colonies, the dermis is seen to lie above extensive subdermal lacunae belonging to both the incurrent and excurrent systems of canals. Surface views of intact specimens reveal a system of such subdermal canals converging upon each oscule. By way of these subdermal canals, water in the interior of the sponge finds its way to the oscules.

The dermis is perforated by pores arranged in ill-defined groups and leading into large subdermal incurrent lacunae. Trabeculae of amoebocytes reinforced with spicules reach the surface at intervals and support the dermal membrane above the extensive subdermal lacunae.

ENDOSOMAL ANATOMY: The interior of the sponge is complicated in structure. Thin sheets or membranes of amoebocytes, anastomosing one with another, separate the extensive interlocking systems of incurrent and excurrent canals. In thin sections, the interior of the sponge has a very porous, open structure, with extensive systems of canals separated by thin membranes of cells. The flagellated chambers are located in the cellular membranes and communicate between the excurrent and incurrent canal systems. The flagellated chambers are ellipsoidal in shape with dimensions varying from 30 x 25μ to 45 x 35μ. The choanocytes vary from 2.5 to 3.5μ across. The chambers appear to be eurypylous, but I am not certain of this at present.

Although most specimens have the loose, open structure described above, some have a denser endosome, the trabeculae of cells being more extensive. The trabeculae are perforated by thin, incurrent canals which open into the flagellated chambers, and these in turn lead into wide excurrent channels.

SKELETON: The chief components of the skeleton are tracts of oxeas running toward the surface and anastomosing at intervals. These tracts contain from several to more than a dozen spicules in cross-section. They occur in the cellular trabeculae which are also reinforced by many spicules of the same sort randomly distributed. Spongin is scarce, occurring in small patches along the spicule tracts.

In many specimens spicule tracts are rare and ill-defined or entirely absent. In these cases all the spicules are arranged at random in the cellular trabeculae.

The dermal spiculation repeats in essence the pattern of the endosomal skeleton. Multispicular tracts, running essentially parallel to one another, occasionally anastomose to divide the dermis up into areas 1 to 2 mm. long and 200 to 300μ wide. In each dermal area bounded by multispicular tracts are imbedded numerous single spicules which intermesh in such a way as to divide the area into many smaller triangular or trapezoidal areas in which the pores open (fig. 8; Pl. 2, fig. 2). In specimens which lack endosomal multispicular tracts such tracts are also weakly developed in the dermis, with intermeshing single spicules making up the surface pattern in the main.

The spicules (fig. 6) are oxeas which taper gradually from the midpoint and rapidly toward the extremities. For example, a spicule 280μ in length was found to measure 9μ in thickness midway along its length; its thickness 90 to 100μ in either direction away from the midpoint was 8μ; the last 40 to 50μ at either end of the spicule tapered rapidly to a point. Variant categories of spicules, such as styles or strongyles, are only occasionally met with in this species.

The spicules are straight or gently curved at the midpoint; in some specimens the central curvature is more pronounced. The spicules vary considerably in size, the mean value for the length and width of the oxeas of 16 New England specimens being (50 measurements per specimen): *285*μ x *7.6*μ. The range of the means is: length, 231 to 328μ; width, 5.7 to 9.8μ. The over-all range of size is: length, 135 to 390μ; width, 3.7 to 13.1μ.

The oxeas of European specimens studied are considerably larger than those of American specimens. Spicule size ranges and means* of six European specimens follow:

* Measurements based on 50 spicules per specimen.

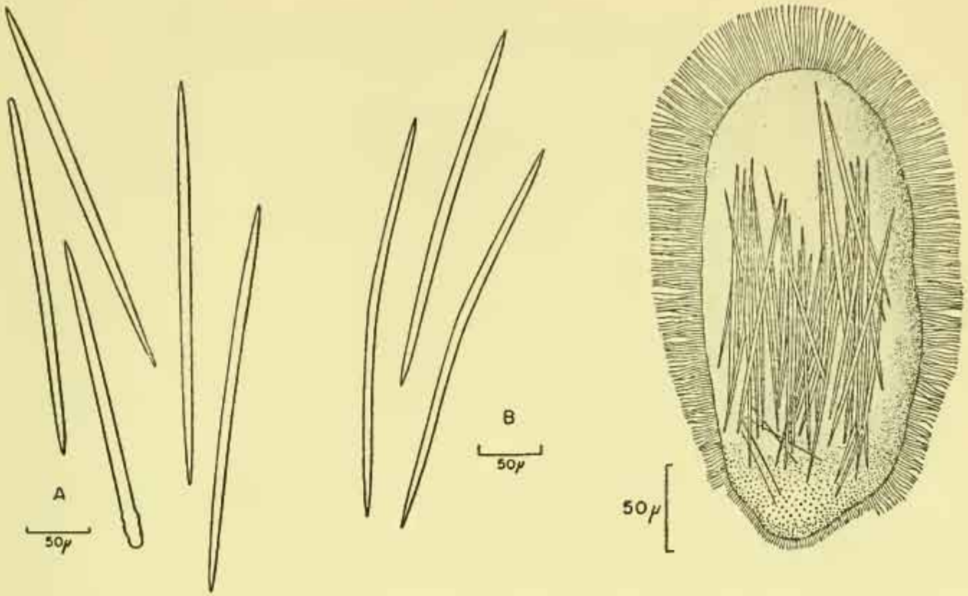


FIGURE 6. Spicules of *Halichondria bowerbanki*. A. Oxeas and styles. New Haven, Conn. YPM #814. B. Oxeas. Double Beach (Branford), Conn. YPM #1819.
FIGURE 7. Larva of *Halichondria bowerbanki*. Milford Harbor, Conn. (Stained whole mount.)

Plymouth, England
YPM No. 2167A: length, 315–*388*–472μ; width, 4–*10*–14μ.
YPM No. 2167B: length, 265–*390*–515μ; width, 6–*11*-15μ.
YPM No. 2168: length, 329–*452*–601μ; width, 8–*12*–18μ.
YPM No. 2169: length, 350–*452*–572μ; width, 6–*13*–17μ.
Range and mean values of all Plymouth specimens:
length, 265–*421*–601μ; width, 4–*12*–18μ.
Étang de Thau, Sète, France
YPM No. 2165: length, 307–*380*–158μ; width, 6–*10*–13μ.
YPM No. 2166: length, 307–*380*–472μ; width, 3–*6*–7μ.
Range and mean values of all specimens from Sète:
length, 307–*380*–472μ; width, 3–*8*–13μ.

The spicules of the dermis and endosome show no conspicuous size difference in New England specimens. Mean values for lengths and widths of oxeas of nine Long Island Sound specimens are: dermis, 289μ x 7.7μ; endosome, 285μ x 7.7μ. Three specimens from southern Massachusetts reveal similar data: dermis, 261μ x 6.3μ; endosome, 264μ x 6.5μ. (See Table 9 for detailed data.) A specimen from Sète, France, is consistent with the American populations in this character. Mean spicule dimensions (length x width) follow: dermis, 376μ x 6μ; endosome,

TABLE 8

SPICULE DIMENSIONS OF *HALICHONDRIA BOWERBANKI*

LOCALITY	SPICULE LENGTH* RANGE AND MEAN DERMIS	SPICULE WIDTH* RANGE AND MEAN DERMIS	SPICULE LENGTH* RANGE AND MEAN ENDOSOME	SPICULE WIDTH* RANGE AND MEAN ENDOSOME
Hammonasset, Conn. YPM #849	238–*289*–336μ	5.3–*8.0*–12.3μ	221–*278*–332μ	4.1–*7.3*–9.0μ
Double Beach (Branford), Conn. YPM #1819	246–*288*–353μ	6.9–*8.6*–10.3μ	213–*287*–349μ	3.7–*8.0*–11.1μ
Double Beach (Branford), Conn. YPM #1867	180–*306*–365μ	4.5–*8.9*–11.5μ	213–*307*–390μ	4.5–*8.6*–12.3μ
Double Beach (Branford), Conn. YPM #1881D	176–*294*–357μ	4.1–*8.5*–11.9μ	205–*309*–357μ	6.2–*9.1*–11.5μ
Double Beach (Branford), Conn. YPM #763	246–*293*–349μ	4.1–*6.2*–9.8μ	213–*308*–381μ	4.5–*7.1*–11.5μ
Double Beach (Branford), Conn. YPM #840	197–*246*–316μ	4.1–*5.7*–7.8μ	197–*253*–332μ	4.1–*5.7*–8.2μ
Double Beach (Branford), Conn. YPM #860	180–*276*–336μ	4.5–*8.0*–11.9μ	185–*272*–353μ	4.1–*7.7*–10.3μ
Lighthouse Pt., New Haven, Conn. YPM #814	250–*288*–328μ	4.5–*7.4*–8.6μ	193–*296*–336μ	4.1–*7.3*–8.6μ
Bass River, Mass. YPM #939	217–*260*–303μ	4.5–*7.0*–8.2μ	180–*260*–312μ	4.1–*6.6*–8.6μ
Lagoon Pond, Martha's Vineyard, Mass. YPM #940A	217–*260*–328μ	4.1–*5.9*–8.2μ	209–*272*–353μ	4.1–*6.5*–8.2μ
Lagoon Pond, Martha's Vineyard, Mass. YPM #940B	205–*263*–308μ	4.1–*6.0*–8.2μ	193–*259*–295μ	4.5–*6.3*–8.2μ

* All measurements based on 50 spicules per specimen.

(Continued)

TABLE 8—Conclusion

SPICULE DIMENSIONS OF *HALICHONDRIA PANICEA*

LOCALITY	SPICULE LENGTH* RANGE AND MEAN DERMIS	SPICULE WIDTH* RANGE AND MEAN DERMIS	SPICULE LENGTH* RANGE AND MEAN ENDOSOME	SPICULE WIDTH* RANGE AND MEAN ENDOSOME
Kent Isl., N. B. YPM #919	156–*237*–287μ	3.7–*5.0*–7.8μ	189–*255*–303μ	4.1–*5.6*–7.8μ
Kent Isl., N. B. YPM #903	156–*260*–324μ	3.3–*8.0*–10.7μ	176–*255*–324μ	3.7–*7.3*–11.1μ
Kent Isl., N. B. YPM #867	144–*212*–296μ	3.3–*4.8*–7.0μ	127–*236*–320μ	4.1–*5.3*–8.2μ
Barter Isl., Maine YPM #1243	180–*240*–353μ	4.5–*7.0*–9.8μ	156–*270*–406μ	3.7–*7.2*–12.3μ
Barter Isl., Maine YPM #1244	189–*300*–373μ	5.8–*8.7*–12.0μ	168–*313*–418μ	4.5–*9.0*–12.3μ
Barter Isl., Maine YPM #1246	164–*265*–377μ	5.0–*7.1*–12.0μ	164–*287*–394μ	4.1–*8.1*–11.1μ
St. Valéry-en-Caux, France YPM #1074	139–*232*–369μ	4.1–*6.8*–10.3μ	172–*296*–406μ	4.1–*8.4*–11.9μ
St. Valéry-en-Caux, France YPM #1075	221–*303*–439μ	4.1–*8.6*–14.8μ	230–*336*–410μ	4.1–*8.8*–13.9μ
Etretat, France YPM #1077	197–*289*–402μ	4.1–*7.7*–12.3μ	201–*313*–402μ	4.9–*8.2*–12.3μ
Roscoff, France YPM #2111A	205–*254*–324μ	3.3–*4.6*–7.4μ	193–*253*–303μ	4.1–*4.6*–7.0μ
Roscoff, France YPM #2111B	217–*254*–312μ	2.1–*4.4*–7.4μ	213–*259*–349μ	3.7–*4.8*–7.8μ
Plymouth, England YPM #2097A	135–*220*–336μ	4.1–*6.3*–10.7μ	176–*242*–340μ	4.1–*7.2*–11.5μ
Plymouth, England YPM #2097B	180–*224*–303μ	4.1–*6.2*–9.0μ	164–*262*–328μ	4.5–*7.5*–11.9μ

* All measurements based on 50 spicules per specimen.

383μ x 6μ. On the other hand, in a specimen from Plymouth, England, the dermal spicules are significantly larger than the endosomal ones. Mean dimensions are: dermis, 425μ x 13μ; endosome, 389μ x 11μ.

Specimens from Connecticut collected in winter and early spring tend to have larger spicules than those collected in summer and early autumn. The ranges and mean length and width measurements of oxeas of specimens collected in winter and summer follow:

Winter (5 specimens): length, 176–*300*–390μ width, 3.7–*8.7*–13.1μ.
Summer (11 specimens): length, 135–*276*–361μ; width, 4.1–*7.0*–12.3μ.

Eggs and larvae: The eggs and larvae of *H. bowerbanki* appear in mid- and late summer in New England. The eggs, subspherical in shape, measure 40 x 37μ to 45 x 40μ in diameter; the nuclei are 16 x 12μ; the nucleoli, 5μ in diameter. Larvae are released from late August (first seen leaving oscules of colonies in Connecticut on Aug. 21) through late November (see Part II). The larvae (fig. 7) are obovoid in shape, 180 to 290μ in length, 100 to 115μ across the widest portion. They are completely flagellated, with the longest flagella (31μ) at the anterior end. At the posterior end is a zone of shorter flagella (8μ). In the interior of the stereogastrulae, at the time of their release, are numerous small oxeas, with length and width measurements varying as follows: 128 to 150μ x 2.5 to 3.0μ.

Winter condition: During the winter, when water temperatures are near 0° C., many colonies of this species remain alive and active in Connecticut; flagellated chambers are present. Some, however, undergo partial degeneration, changing color as noted above, and losing their flagellated cells. Such colonies are composed chiefly of masses of amoebocytes. In May, flagellated chambers reappear and the colonies resume an active life. There is no evidence of gemmule formation in this species.

Distribution in America: *Halichondria bowerbanki* is an abundant sponge along the Connecticut coast of Long Island Sound. It occurs from about half a foot above mean low water down into subtidal waters. Occasional specimens can be found in tide pools up to the mid-tide region. It is commonly found attached to sea weeds and also grows on the upper surfaces, sides and undersides of rocks. I have collected it intertidally at Hammonasset State Park (Meig's Point); Stony Creek; Pine Orchard; Double Beach (Branford); Lighthouse Point (New Haven); Bradley Point (West Haven); and Milford. It also occurs in the offshore waters of Long Island Sound down to depths of at least ten meters. It is not found in the deeper waters of Block Island Sound.

Its range extends northward to the southern shores of Massachusetts. There I have collected it in Lagoon Pond, Martha's Vineyard, and at Bass River, Cape Cod. Verrill (*in:* Verrill and Smith, 1873, p. 743) recorded it from Long Island Sound near New Haven and from Vineyard Sound, Mass., as *"Halichondria?* species undetermined, b."

Discussion: *Halichondria bowerbanki* differs from *H. panicea* in the following characters which will be discussed in greater detail below: 1) external form; 2) dermal spiculation, both in arrangement and size of spicules; 3) larval structure and season of reproduction. In other characters, such as spicule form and dimensions, pore size, and oscular size, the two species overlap.

A comparative study has been made of specimens of *H. bowerbanki* from southern New England; Plymouth, England; and Sète, France, and of specimens

TABLE 9

SUMMARY OF DERMAL AND ENDOSOMAL SPICULE DIMENSIONS IN *HALICHONDRIA*

SPECIES AND LOCALITY	NUMBER OF SPECIMENS	SPICULE LENGTH RANGE AND MEAN DERMIS	SPICULE WIDTH RANGE AND MEAN DERMIS	SPICULE LENGTH RANGE AND MEAN ENDOSOME	SPICULE WIDTH RANGE AND MEAN ENDOSOME
H. bowerbanki Long Island Sound	9	176–*285*–365μ	4.1–*7.7*–12.3μ	185–*289*–390μ	3.7–*7.7*–12.3μ
H. bowerbanki Southern Massachusetts	3	205–*261*–328μ	4.1–*6.3*–8.2μ	180–*264*–353μ	4.1–*6.5*–8.2μ
H. bowerbanki Sète, France	1	322–*376*–450μ	4–*6*–7μ	307–*383*–472μ	3–*6*–7μ
H. bowerbanki Plymouth, England	1	315–*425*–493μ	8–*13*–16μ	300–*389*–472μ	7–*11*–15μ
H. panicea Europe	8	135–*254*–439μ	2.1–*6.4*–14.8μ	164–*280*–410μ	4.1–*7.1*–13.9μ
H. panicea Denmark (Brøndsted, 1929*)	1	192–*326*–456μ	.....	168–*347*–456μ	.....
H. panicea Maine and New Brunswick	6	144–*252*–377μ	3.3–*6.8*–12.0μ	127–*269*–418μ	3.7–*7.1*–12.3μ

* Biometrische Studien über Schwämme. I. Vidensk. Medd. dansk naturh. Foren. Kbh., vol. 88, 1–13.

TABLE 10

LARVAL CHARACTERISTICS OF *HALICHONDRIAS*

SPECIES, LOCALITY, AUTHOR	SEASON OF LARVAL RELEASE	RANGE OF TOTAL LENGTH	RANGE OF MAXIMUM WIDTH	LENGTH OF CILIA, ANT. END	LENGTH OF CILIA, POST. END	RANGE OF SPICULE LENGTH AND WIDTH
H. panicea Roscoff (Topsent, 1911)	May, June	484–517μ	165–187μ	15μ	8μ	60–70μ Width–?
H. panicea Plymouth (Hartman)	?	357μ	99μ	9μ	?	70μ x 0.9μ
H. bowerbanki Long Island Sound (Hartman)	August-November	183–289μ	102–113μ	31μ	8μ	128–150μ x 2.5–3.0μ
H. bowerbanki Roscoff (Topsent, 1911)	August-September	330–440μ	175–250μ	20–23μ	35–40μ	130–140μ Width–?

of *H. panicea* from Plymouth, England; Roscoff and St. Valéry-en-Caux, France; and the coasts of Maine and New Brunswick in North America. In such a study, one is immediately impressed by differences in external form. Mature colonies of *H. bowerbanki* tend to be highly ramose, although some are flabellate. Young colonies of this species (Pl. 4, figs. 4, 5) are encrusting and some show a tendency to produce many low oscular tubules; such colonies show some resemblance to colonies of *H. panicea* figured by Bowerbank (1874, Pl. 39, figs. 4, 5). But the type of encrusting colonies of *H. panicea* with rows of oscules raised on ridges or tubules, as figured by Bowerbank (1874, Pl. 40, figs. 3, 4) and represented in the Peabody Museum collections by specimens from France are not found in populations of *H. bowerbanki*. Older encrusting colonies of *H. panicea* frequently bear more or less regularly spaced taller oscular tubules (*see*, e.g., Johnston, 1842, Pl. 11, fig. 5; Bowerbank, 1874, Pl. 40, fig. 2; Vosmaer, 1933–35, Pl. 59, fig. 10; Burton, 1928, fig. 1a; specimens in the Peabody Museum collections from Plymouth, England, and the coast of Maine). Colonies of this form are lacking in *H. bowerbanki*, in which the branches of older specimens are taller and much more erratic in growth. The "cockscomb" variety of *H. panicea* figured by Bowerbank (1874, Pl. 40, fig. 5) is approached by flabellate colonies of *H. bowerbanki* (Pl. 3, fig. 11), but these lack the apical rows of papillae shown in Bowerbank's figure. One specimen of *H. bowerbanki* (Pl. 4, fig. 2) has a chimney-like outgrowth resembling those figured by Bowerbank (1874, Pl. 39, fig. 1) and Burton (1928, fig. 1d) in *H. panicea;* in *H. bowerbanki*, however, the chimney is not solitary but is located in the center of a colony otherwise showing the branching habit characteristic of the species. The young branching colonies of *H. panicea* illustrated by Renouf (1936, fig. 2) do show a striking resemblance to colonies of *H. bowerbanki*. Regrettably Renouf gives no structural details to indicate whether his specimens overlap in other characteristics with populations of *H. bowerbanki*. The curious colony type with long, thin branches figured by Vosmaer (1933–35, Pl. 60, fig. 4) and Grentzenberg (1891, fig. 2) is represented by several specimens from Connecticut which, however, show a greater tendency toward anastomosis of the branches (Pl. 4, figs. 6, 7, 8).

In summary, it may be said that in regard to colony form, the two species, *H. panicea* and *H. bowerbanki*, overlap to some extent, but that some of the colony shapes most characteristic of *H. panicea* are not represented in populations of *H. bowerbanki*. The typical branching form of *H. bowerbanki*, on the other hand, is not found regularly in *H. panicea*.

A striking difference between *H. panicea* and *H. bowerbanki* is seen in the dermal skeleton. Surface views of *H. panicea* reveal a very regular network of multispicular tracts which divide the dermis into chiefly oblong areas, in which the closely spaced pores open (fig. 9; Pl. 2, fig. 1). Occasional isolated spicules lie across the areas. The spicule tracts are from 30 to 90μ in width and the dermal areas between them vary from 90 to 150μ in greater diameter. This very characteristic pattern is apparent in specimens which I have examined from Plymouth, England; Roscoff, France; and the coast of Maine.

The dermal spiculation of *H. bowerbanki*, as described above, is quite different (fig. 8; Pl. 2, fig. 2). Multispicular tracts, when present, are widely spaced and divide up the dermis into larger areas, 1 to 2 mm. long and 200 to 300μ wide. These areas are further subdivided by a pattern of overlapping individual spicules. The pores are widely spaced. This is the most useful character for separating these two species; in my experience, it has proved consistent and reliable

for both American and European populations. Burton (1930b) comments that the dermal reticulation of *H. bowerbanki* is more strongly marked than that of *H. panicea.*

The dermal spicules of *H. bowerbanki* are approximately the same size as the endosomal spicules. One specimen from Plymouth, England, is anomalous in this regard, however, and has dermal spicules which are noticeably larger than those of the endosome. In specimens of *H. panicea* from both New England and Europe, the dermal spicules are consistently smaller than those of the endosome. Data for these characters are summarized in Table 9. Fifty measurements were made for each specimen. A detailed tabulation of these data is given in Table 8.

Vosmaer (1933–35) gives an excellent account of the ectosomal anatomy of *H. panicea,* pointing out the variation which occurs. In all specimens cellular pillars reinforced with tracts of spicules run to the dermis from the endosome. These spicular tracts fan out at the surface to join the dermal tracts. The ectosomal skeletal architecture of *H. panicea* suggested to Dr. G. P. Bidder "the vaulted interior of a Gothic crypt" (personal communication). In some specimens the pores open into small subdermal cavities separated by pillars of cells and these cavities open below into much larger lacunae or "crypts" (Vosmaer's term) leading into narrower inhalant canals which ramify the endosome. In other specimens the small subdermal cavities are absent, and the pores lead directly into large lacunae.

The ectosomal anatomy of *H. bowerbanki* resembles the latter arrangement, with the pores opening directly into extensive lacunae which spread out horizontally beneath the dermis. The pillars of cells and spicules supporting the dermis are thin and are generally reinforced by relatively few spicules. Bidder's simile is hardly appropriate for the weak skeletal architecture in the ectosome of *H. bowerbanki.*

Other conspicuous differences between *H. bowerbanki* and *H. panicea* concern the structure of the larvae and the season of reproduction. Data comparing the two species in these regards are given in Table 10. See also figures 7 and 33.

Chronic lumpers such as Vosmaer (1933–35) would have little trouble in including *H. bowerbanki* in a broad concept of *H. panicea.* There is no doubt that the two species overlap in many characteristics. Both species are highly variable in structure and form and hence separating them is a difficult matter. The discussion above focuses attention on a series of characters which, in my experience, represent consistent differences between the species and on which I have based my conclusion that the two species are separate and distinct. The dermal skeletal pattern and the structure of the larvae seem to be the most reliable distinguishing features. Vosmaer, however, was even reluctant to accept larval differences as being significant. He states (1933–35), "I for my part have no doubt that the larvae will be found just as variable as the adult sponges."

Although the shape and appearance of colonies of *H. bowerbanki* from America and Europe show good agreement, as does the structure of the dermal skeleton, specimens from populations on opposite sides of the Atlantic do exhibit certain differences. It has already been pointed out that the spicules of specimens from England and France are significantly larger than those of New England colonies. There is also a difference in larval structure, bearing out in some measure the comment of Vosmaer quoted above. The larvae of *H. bowerbanki* from Roscoff, France, figured by Topsent (1911), are larger than those found by the present writer in specimens from the Connecticut population. The pattern of the larval

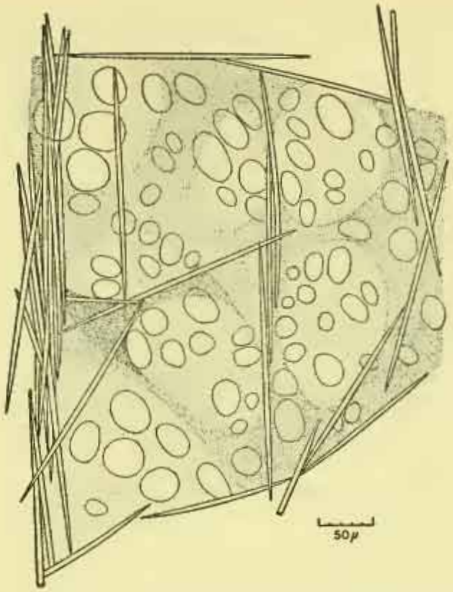


FIGURE 8. Portion of dermis of *Halichondria bowerbanki* showing characteristic arrangement of skeleton and pores. Lightly shaded areas represent openings from subdermal cavities into channels leading to the interior of the sponge. More heavily shaded areas represent trabeculae of cells extending from dermis to interior. Lagoon Pond, Martha's Vineyard, Mass. YPM #940.

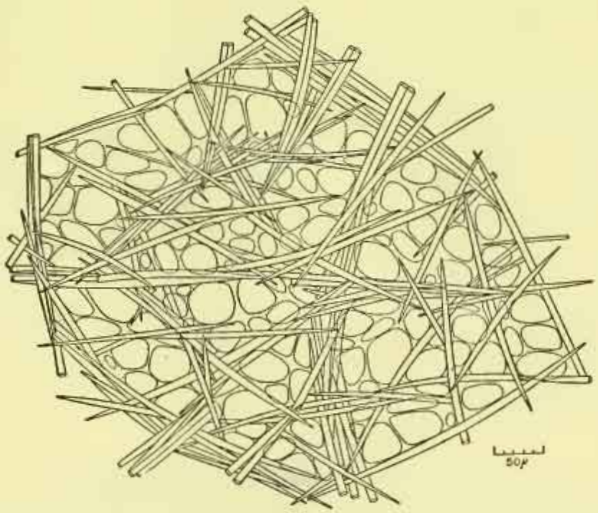


FIGURE 9. Portion of dermis of *Halichondria panicea* showing characteristic arrangement of skeleton and pores. Plymouth, England. YPM #2097.

flagella also differs. The posterior flagella of Topsent's specimens form a long tuft, while those of Connecticut larvae are short. See Table 10 and figure 7. The breeding seasons are similar on both sides of the Atlantic. It is highly probable that the American and European populations represent valid subspecies; subspecific names are not proposed at the present writing, since data from a larger series of specimens from Europe are needed.

Some colonies of *H. bowerbanki* bear a resemblance in external form, spicule dimensions and oscular size to Swartschewsky's (1905) figure of *Halichondria grossa* Schmidt. The former author makes no reference to the characters used in my diagnosis of *bowerbanki,* however, and it is difficult to draw a detailed comparison of the species. Swartschewsky states that the oxeas are arranged in a disorderly fashion, only rarely being grouped into more or less long, thick clusters, running in all directions in the endosome. This describes the condition of the endosomal skeleton of some specimens of *H. bowerbanki* fairly well. Whether or not *bowerbanki* and *grossa* are synonyms cannot be answered on the basis of our present, incomplete knowledge of the latter species.

Swartschewsky's figure of *Halichondria luxurians* (Lieberkühn) also resembles certain colony types of *H. bowerbanki.* However, *H. luxurians* has styles, tylostyles, and strongyles as spicules.

The taxonomic status of *H. bowerbanki* (which has been referred to as *H. coalita* in most of the literature on the species) has been clarified by Burton (1930b). The name *"coalita"* was first used by Müller (1776, p. 256) who cited as his type a specimen figured by Ellis (1755, p. 80, Pl. 32, fig. F). Burton has pointed out correctly that Ellis' figure represents a specimen of *Haliclona oculata* (Pallas, 1766). Burton has shown further that most subsequent references to *coalita* concern *Haliclona oculata* or *Halichondria panicea* or are unrecognizable. To my knowledge Fleming (1828, p. 522) was the first author to refer *coalita* to the genus *Halichondria,* but he cites Müller's (1776) original incorrect designation. The name *"coalita"* is thus unavailable for use with *Halichondria.* Johnston (1842, p. 135) very probably had reference to the *Halichondria* in question, but he also applied Müller's name. Bowerbank (1866, 1874) likewise used the name, *"coalita,"* citing Johnston as the author of the species. Bowerbank's specimen was a gift from Grant whose many references (1825, 1826a, 1826c, 1827) to *Spongia coalita* without indication doubtless concern the species under discussion.

Bowerbank (1866, p. 239) suggests that Esper's (1794, Pl. 41) *Spongia suberosa* "is undoubtedly the same species as that designated *Spongia coalita* by Dr. Grant, and *Halichondria coalita* by Johnston." I have been unable to consult Esper's paper at this writing, but the possibility exists that *suberosa* is an available name for the species in question. However, Ehlers (1870) does not mention this species in his restudy of Esper's sponges, and it is probable that the specimen is lost. Indeed, Bowerbank's specimen of *Halichondria coalita* is apparently the only one still extant of those described by early authors. Burton has wisely chosen this specimen, figured by Bowerbank in 1874 (Pl. 41, fig. 18), as the type for his new species, *Halichondria bowerbanki.*

Order Poecilosclerina

Family Microcionidae Hentschel

Microciona prolifera (Ellis and Solander, 1786) Verrill, 1873

Synonymy:

Spongia prolifera Ellis and Solander, 1786, p. 189

Spong[i]a ostracina Rafinesque, 1819, p. 150
[non] *Spongia prolifera* Grant, 1826a, pp. 115, 116, 123, and 1827, pp. 135, 138
Spongia urceolata Desor, 1851, p. 67
Microciona prolifera, Verrill, *in:* Verrill and Smith, 1873, p. 741
Clathria delicata Lambe, 1896, p. 192

Discussion: This well known sponge is abundant in Long Island Sound where it grows commonly on oysters, beginning life as a thin encrustation. As the sponge ages, vertical finger-like lobes develop (Pl. 4, fig. 11); in old colonies these increase in number and anastomose to form bushlike colonies with the branches intricately interwoven (Pl. 4, fig. 9). Such colonies often reach a large size; the largest one collected on an oyster bed by the present writer measures 20 cm. in height and spreads out 25 cm. in one direction and 8 cm. in the other. Often flattened branches arise from the basal encrustation, producing fan-shaped structures which break up into lobes distally (Pl. 4, fig. 10, 13). In extreme cases, such flattened branches form cup-shaped colonies by growing up from the substratum in a circular pattern (Pl. 4, fig. 14). Desor (1851) also mentions this colony type.

M. prolifera occurs from mean low water down to depths of at least ten meters in the New Haven area. It is occasionally found in tide pools up to two feet above mean low water. Intertidally this sponge grows on the upper surfaces, the sides, and the undersides of rocks. Intertidal individuals are chiefly encrusting or have lobes no more than two or three cm. in height. The sponge is perennial in growth in Long Island Sound in both offshore and intertidal locations, but individuals growing in the latter environment undergo considerable degeneration during the winter and die back to thin encrustations which renew growth in the spring. Large, bushy colonies which require several years of growth to assume this form, seldom, if ever, are found near mean low water.

The color of *M. prolifera* varies seasonally and with exposure to light. In the summer and autumn most specimens are tomato red (Maerz and Paul, 1950, Pl. 3, H-12) or terra cotta (Pl. 4, D-12, E-12, and H-12) in color; others are burnt orange (Pl. 3, F-12) or burnt sienna (Pl. 5, G-12). In winter and spring many specimens are browner in color, near gold brown (Pl. 14, E-10, B-11; Pl. 15, E-10) or henna (Pl. 6, G-12); others approach burnt sienna (Pl. 5, J-12) or terra cotta (Pl. 4, B-12). The redder hues are characteristic of colonies exposed to the light; colonies growing on the undersides of rocks are nearer orange brown in color.

The general morphology of this sponge has been described by Wilson (1912) and George and Wilson (1919). The present writer has little to add, except to point out the occurrence of cords of elongate cells in which the developing spicules are aligned. These structures were noted in small regenerating colonies fixed and stained by Patricia J. Harris, of the Bingham Oceanographic Laboratory. Cell cords of this general nature are apparently of wide occurrence in the Demospongiae, having been noted by Herlant-Meewis (1949) in *Spongilla* and *Suberites domunculus* and by the present author in several species of *Haliclona* as well as *Microciona*.

Table 11 compares the sizes of spicules from Long Island Sound specimens with those reported from other localities along the American Atlantic Coast. Three categories of megascleres (fig. 10A) occur: (1) The most abundant ones are long, stout, subtylostyles (less frequently styles) with smooth shafts and spiny, or occasionally smooth, heads (the heads may be unspined). These spicules project

TABLE 11

SPICULE DIMENSIONS OF *MICROCIONA PROLIFERA*

LOCALITY	RANGE AND MEAN VALUE OF SPICULE DIMENSIONS				
	THICK SUBTYLOSTYLES	THIN SUBTYLOSTYLES	SPINY SUBTYLOSTYLES	TOXAS	CHELAS
Prince Edward Isl., (Lambe, 1896)	196–353μ x 13μ	157–262μ x 3μ	72–242μ x 9μ	26–58μ	13μ
Mt. Desert Isl., Maine (Procter, 1933)	243–*284*–324μ	284–405μ (spiny subtylostyles)	105–*145*–203μ	—	12.1μ
Woods Hole, Mass. (Procter, 1933)	109–363μ	—	60–*79*–90μ	30μ (extremely rare)	12–*15*–16.5μ
Woods Hole, Mass. (de Laubenfels, 1949)	175μ x 7μ	100–150μ x 1–5μ	90μ x 7μ	10–40μ	15μ
Double Beach (Branford), Conn. YPM #1912E	168–*256*–373μ* x 10.7–*12.3*–15.6μ	115–*205*–344μ* x 2.0–*3.6*–7.0μ	74–*93*–119μ* x 4.5–*7.1*–9.8μ	11–*17*–25μ**	16–*17*–19μ**
Double Beach (Branford), Conn. YPM #1960E	185–*251*–340μ* x 8.6–*12.4*–16.0μ	131–*204*–283μ* x 2.1–*3.6*–5.3μ	74–*91*–111μ* x 5.3–*6.9*–8.2μ	13–*17*–22μ**	14–*16*–19μ**
Lighthouse Pt., New Haven, Conn. YPM #754	115–*234*–362μ** x 7.3–*10.2*–13.9μ	84–*157*–285μ** x 1.8–*2.9*–4.4μ	65–*83*–97μ** x 7.3–*8.8*–11.0μ	11–*21*–40μ**	13–*16*–18μ**

* Measurements based on 50 spicules per specimen.
** Measurements based on 25 spicules per specimen.

(Continued)

TABLE 11—Concluded

SPICULE DIMENSIONS OF *MICROCIONA PROLIFERA*

LOCALITY	RANGE AND MEAN VALUE OF SPICULE DIMENSIONS				
	THICK SUBTYLOSTYLES	THIN SUBTYLOSTYLES	SPINY SUBTYLOSTYLES	TOXAS	CHELAS
Beaufort Harbor, North Carolina (Wilson, 1912)	160–400μ x 8–10μ	Considered developmental stages	80μ x 5–6μ	16–24μ	12–14μ
Beaufort Harbor, North Carolina (George and Wilson, 1919)	Encrusting colony: 150–500μ x 8–12μ Lobe of young colony: 150–380μ x 8–14μ Lobe of old colony: 150–380μ x 8–16μ	Considered developmental stages	80–100μ x 6–8μ	10–40μ	12–16μ

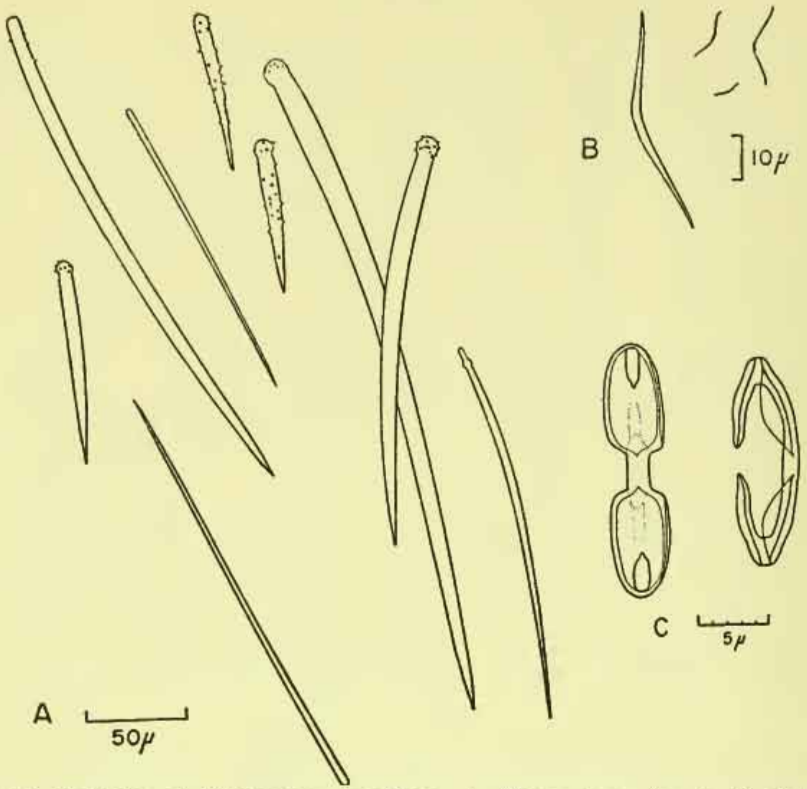


FIGURE 10. Spicules of *Microciona prolifera*. A. Megascleres (see text). B. Toxas. C. Isochelas. New Haven, Conn. YPM #754. Isochelas from specimen from Double Beach (Branford), Conn. YPM #1912E.

laterally from the fibers of the sponge, forming tufts at the surface where the fibers end. (2) Thin subtylostyles and styles, usually with microspined heads. Wilson (1912) and George and Wilson (1919) regard this category of spicules as developmental stages. The shorter ones of these are distributed throughout the sponge and doubtlessly do represent immature spicules. The longer ones, however, are localized chiefly in tufts at the surface and probably represent a distinct category. This hypothesis is supported by the gap in width measurements between the thin and stout types of megascleres. (3) Short acanthosubtylostyles and acanthostyles, in which both shafts and heads are spined, the latter more thickly. These spicules stand out at right angles from the fibers (pointed ends outward) in the interior of the sponge colony. In addition there are two categories of microscleres: (1) palmate isochelas (fig. 10C) and (2) toxas (fig. 10B). The latter are always common in specimens from the New Haven area, although they are rare or absent in specimens north of Cape Cod. Most of the toxas in New Haven colonies are very short (12-20μ) but a few range up to 50-60μ in length.

The available data suggest that the sizes of the short, spiny subtylostyles and toxas increase in northern waters, but there is no apparent correlation of sizes of the other megasclere types or chelas with latitude. George and Wilson (1919) report an increase in width of the large subtylostyles in old portions of colonies.

Vosmaer (1933) regards *Microciona prolifera* as a cosmopolitan species, but his extensive synonymies are highly questionable.

DISTRIBUTION: Nova Scotia and Prince Edward Island to South Carolina, Louisiana and Texas (?).

Prince Edward Island (Lambe, 1896, p. 12, as *Clathria delicata*); Nova Scotia (Lambe, 1900b, p. 160, as *Clathria delicata*); Mt. Desert Isl., Me., 24m. (Procter, 1933, p. 104); Portland, Me. (Lambe, 1896, p. 192, as *Clathria delicata*); Bass Rocks, Cape Ann, Mass., mean low water (Hartman); Edgartown Harbor, Martha's Vineyard, Mass., 8 meters (Desor, 1851, p. 67, as *Spongia urceolata*); Vineyard Sound, Mass., low water to 20 meters (Verrill, *in:* Verrill and Smith, 1873, p. 742; 1880, p. 232); Woods Hole, Mass., and vicinity, low water to 26 meters (Sumner *et al.*, 1913, p. 559; Allee, 1923, p. 175; Procter, 1933, p. 104; de Laubenfels, 1949, p. 12); Long Island Sound, low water to 20 meters (Verrill, *in:* Verrill and Smith, 1873, p. 742; 1880, p. 232; Hartman); shores of Long Island (Rafinesque, 1819, p. 150, as *Spongia ostracina*); Great Egg Harbor, N. J. (Verrill, *in:* Verrill and Smith, 1873, p. 742); coast of New Jersey (Ellis and Solander, 1786, p. 189, as *Spongia prolifera*); Chesapeake Bay, 13 meters (Cowles, 1931, p. 329); Ft. Macon, N. C. (Verrill, *in:* Verrill and Smith, 1873, and Coues and Yarrow, 1879, p. 312); Beaufort Harbor, N. C. (Wilson, 1912, p. 3; George and Wilson, 1919, p. 157; McDougall, 1943, pp. 331-332; de Laubenfels, 1947, p. 35); South Carolina (Verrill, *in:* Verrill and Smith, 1873, p. 742; Hopkins, 1956b, p. 24); Louisiana and Texas (Hopkins, 1956a, p. 44, records an encrusting *Microciona* from these states, but does not identify it as *prolifera*.).

FAMILY MYXILLIDAE Hentschel

Lissodendoryx isodictyalis (Carter, 1882) Topsent, 1897

SYNONYMY:

Halichondria isodictyalis Carter, 1882, p. 285
Tedania leptoderma Topsent, 1889, p. 49
Lissodendoryx leptoderma, Topsent, 1894, p. 35
Lissodendoryx isodictyalis, Topsent, 1897, p. 456
Lissodendoryx carolinensis Wilson, 1912, p. 11

DISCUSSION: This species is widely distributed in subtropical and tropical seas (West Indies, Mediterranean Sea, and East Indies) and extends northward along the Atlantic Coast of North America from the Florida Keys to Woods Hole, Mass. It occurs chiefly as a fouling organism on wharf piles in the region from Beaufort, North Carolina, to Woods Hole, and has been collected near mean low water as an encrustation on rocks at Double Beach (Branford), Connecticut.

The morphology of this sponge has been described by Wilson (1912, p. 11), George and Wilson (1919, p. 150), and de Laubenfels (1936, p. 93). Variations in spicule dimensions are presented in Table 12. Specimens (*carolinensis* type) from the Atlantic Coast of North America from Beaufort, N. C. to Woods Hole are characterized by the presence of large sigmas (mean chord length, 29.3μ) and small chelas (mean chord length, 18.9μ) in contrast to specimens (*isodictyalis* type) from subtropical American waters which have small sigmas (mean chord length, 18.0μ) and large chelas (mean chord length, 21.5μ). Both of these variations occur together in the Mediterranean, however, and this observation is of questionable value for differentiating two subspecies on the American coast.

One specimen of *Lissodendoryx isodictyalis* from Long Island Sound was collected by Verrill in 1874. No more exact locality was given by Verrill, but it is probable that the specimen came from the eastern end of the Sound, since reference to the list of dredging stations of the U. S. Fish Commission for 1874 indicates that no stations were worked west of Saybrook, Connecticut, during that year. Verrill's specimen is massive in form and measures 42 x 30 x 15 mm. in linear dimensions.

Recently *L. isodictyalis* has been found by the present writer at Double Beach (Branford), Connecticut, growing as thin encrustations on rocks. Portions of two colonies were collected in November, 1955; one was growing near the mean low water level, another, about half a foot below. By January, 1956, the remainder of these colonies had the form of elongate encrustations about 8 x 3 cm. in dimensions. Their color in life was light olive tan (Maerz and Paul, 1950, Pl. 12, F-2, G-2). In each, the surface was raised into numerous low knob-like projections which in one case were no higher than 0.5 mm., in the other, about 2 mm. The oscules were about 0.5 mm. in diameter. Spicule dimensions for these specimens are given in Table 12. (See also fig. 11.) In August, 1956, another encrusting colony was collected, 4.5 x 4.5 cm. in dimensions (see Pl. 4, fig. 12); this colony is provided with numerous translucent papillae, 1.5 to 2.5 mm. high and 0.5 mm. in diameter. A large colony, 8 x 8 cm., was observed at the same locality in November, 1956.

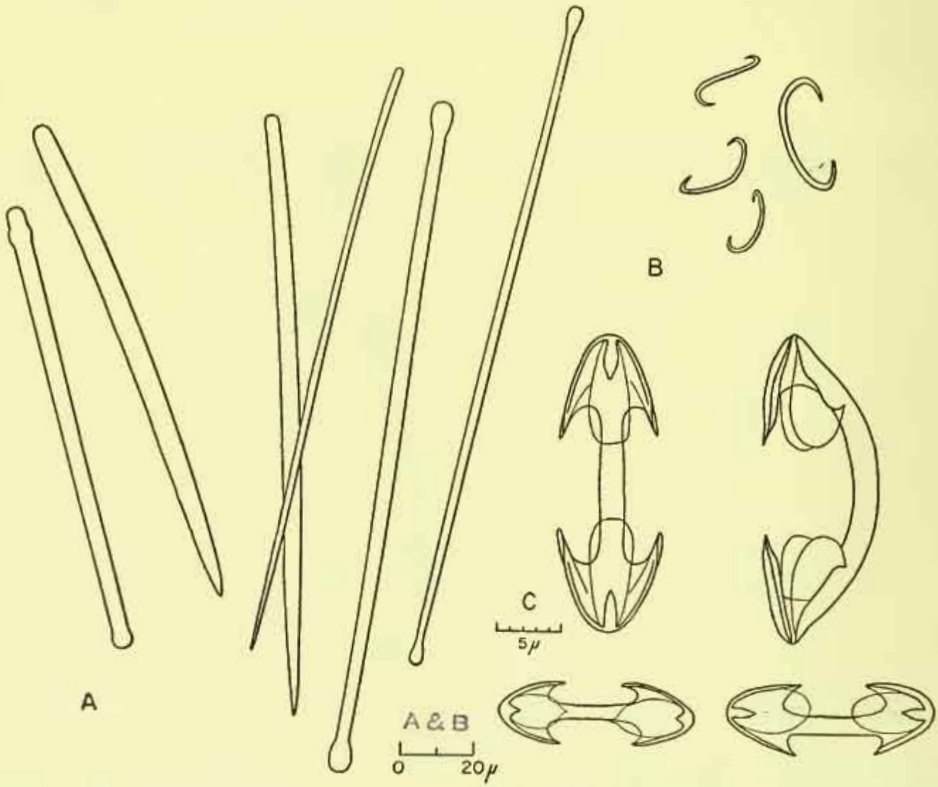


FIGURE 11. Spicules of *Lissodendoryx isodictyalis*. A. Megascleres: styles and tylotes. B. Sigmas. C. Isochelas. Long Island Sound. YPM #2117.

TABLE 12

SPICULE DIMENSIONS OF *LISSODENDORYX ISODICTYALIS*

LOCALITY AND AUTHOR	RANGE OR RANGE AND MEAN OF SPICULE LENGTH X WIDTH		RANGE OR RANGE AND MEAN OF SPICULE LENGTH	
	Styles	*Tylotes*	*Sigmas*	*Chelas*
Woods Hole, Mass. (Hartman; specimen from M. D. Burkenroad) YPM #931**	136–*147*–163μ x 3.7–*4.4*–6.6μ	160–*175*–187μ x 3.3–*4.0*–4.8μ	20–*29*–38μ	15–*22*–26μ
Eastern Long Isl. Sound (Hartman; A. E. Verrill colls.) YPM #2117**	167–*180*–191μ x 1.5–*5.1*–7.0μ	189–*200*–224μ x 2.6–*4.4*–5.1μ	22–*29*–38μ	15–*19*–24μ
Double Beach, Conn. (Hartman) YPM #2037F-2*	148–*176*–197μ x 6.2–*7.5*–8.2μ	164–*183*–197μ x 4.1–*5.0*–6.6μ	21–*26*–43μ	16–*22*–25μ
Double Beach, Conn. (Hartman) YPM #2037F-1*	139–*163*–185μ x 6.1–*7.6*–8.2μ	148–*174*–205μ x 4.5–*5.2*–7.4μ	21–*28*–43μ	16–*22*–25μ
Beaufort, N. C. (Hartman; specimen from I. M. Newell) YPM #616**	162–*243*–316μ x 4.4–*7.0*–9.2μ	159–*178*–191μ x 4.4–*5.5*–7.3μ	24–*32*–38μ	13–*16*–25μ
Beaufort, N. C. (George and Wilson, 1919)	160–180μ x 5–8μ	160–190μ x 5μ	18–36μ	12–26μ
Fort Jefferson, Fla. (de Laubenfels, 1936)	145μ x 5μ	175μ x 4μ	18μ	21μ
Harrington Sound, Bermuda (Hartman; specimen from W. Bergmann) YPM #699**	136–*152*–163μ x 2.6–*3.3*–3.7μ	176–*192*–207μ x 2.6–*3.1*–3.7μ	17–*18*–20μ	20–*22*–24μ
Bermuda (de Laubenfels, 1950)	150μ x 3–5μ	180μ x 2–4μ	12–*17*–20μ	22μ

* Fifty of each category of megascleres measured; 25 of each category of microscleres measured.
** Twenty of each category of megascleres measured; 10 of each category of microscleres measured.

(Continued)

TABLE 12—Concluded

SPICULE DIMENSIONS OF *LISSODENDORYX ISODICTYALIS*

LOCALITY AND AUTHOR	RANGE OR RANGE AND MEAN OF SPICULE LENGTH x WIDTH		RANGE OR RANGE AND MEAN OF SPICULE LENGTH	
	Styles	*Tylotes*	*Sigmas*	*Chelas*
Acapulco, Mexico (TYPE: Carter, 1882)	168μ x 6.3μ	200μ x 6.3μ	17μ	25μ
Guadeloupe (Topsent, 1889)	160–175μ x 3–6μ	198–210μ x 4–5μ	25–30μ	25–30μ
Monaco (Topsent, 1925a)	150–170μ	180–190μ	28–32μ	14–16μ
Naples (Topsent, 1925a)	230–280μ x 2–6μ	265–310μ x 3–5μ	25–31μ	29–33μ
Venice, Italy (Topsent, 1925a)	215μ	200μ	33–35μ, 55μ	25–27μ
Amboina, Moluccas (Topsent, 1925a)	180–200μ x 5–7μ	200–215μ x 5–6μ	25–30μ	30–31μ
Celebes (Topsent, 1925a)	200μ x 5–6μ	220μ x 5–6μ	22μ	30μ

DISTRIBUTION IN NORTH AMERICA AND THE CARIBBEAN SEA: Woods Hole, Mass., to the Florida Keys; Bermuda; West Indies; Venezuela; Acapulco, Mexico.

Woods Hole, Mass. (Hartman—specimen collected by M. D. Burkenroad); eastern Long Island Sound (Hartman—specimen collected by A. E. Verrill); Double Beach (Branford), Conn. (Hartman); Beaufort, N. C. (Wilson, 1912, p. 11, as *L. carolinensis;* George and Wilson, 1919, p. 150, as *L. carolinensis;* McDougall, 1943, p. 331, as *L. carolinensis;* de Laubenfels, 1947, p. 35; Hartman—specimens collected by I. M. Newell); South Carolina (Hopkins, 1956b, p. 24); Fort Jefferson, Florida (de Laubenfels, 1936, p. 93); Bermuda (de Laubenfels, 1950, p. 73); Guadeloupe (Topsent, 1889, p. 49, as *Tedania leptoderma*); Puerto Cabello, Venezuela (Carter, 1882, p. 285, as *Halichondria isodictyalis*); Acapulco, Mexico (Carter, 1882, p. 285, as *Halichondria isodictyalis*).

ORDER HAPLOSCLERINA

FAMILY DESMACIDONIDAE Gray

Isodictya Bowerbank 1863, emend.

The genus *Isodictya* was first mentioned by Bowerbank in 1859 in a general paper on the anatomy and physiology of sponges, in which he figured spicules

of two species of the genus. A spicule of *Isodictya anomala* Bowerbank, MS (*sic*) was figured to illustrate the "inflato-fusiformi-acerate" category of spicules (pp. 286, 323, Pl. 23, fig. 11); a spicule of *Isodictya lobata* Bowerbank, MS (*sic*) was figured to illustrate the "dentato-palmate inequi-anchorate" category of spicules (p. 327, Pl. 24, fig. 58). No definition of either the genus *Isodictya* or the species *anomala* and *lobata* was given by Bowerbank at that time. Thus, the generic name, *Isodictya,* was not validated in this early paper, although the species *anomala* and *lobata* must stand from this date in accordance with Article 27a in the International Rules of Zoological Nomenclature.

Bowerbank defined and described *Isodictya* in 1863 stating at this time that *"Isodictya infundibuliformis* is perhaps the most perfect type of the genus." In 1864 he repeated the same definition of the genus, including the statement about *I. infundibuliformis* and in addition, he clearly designated *I. palmata* and *normani* as the type species of the genus. It follows that Bowerbank did not intend to designate *infundibuliformis* as the type species by his reference to it in 1863 but was using the word "type" in a different sense. *Isodictya palmata,* therefore, is the type species of the genus by designation of the original author, a conclusion accepted by Dendy (1924, p. 334). Burton (1936, p. 143) has implied that *Isodictya* must be reserved for *anomala* and another name chosen for *palmata;* this seems inadmissable to me.

Bowerbank included a large number of species in the genus *Isodictya;* most of these have since been transferred to other genera. If the above comments are accepted, the name *Isodictya* must be restricted to species allied to *palmata.* Lundbeck's definition of *Homoeodictya* (1905) is an acceptable one for *Isodictya* in this sense, except for its restriction to forms with diactinal megascleres. Evidence is presented in the following pages which argues for an extension of the concept of *Isodictya* to include species with monactinal megascleres, otherwise answering Lundbeck's diagnosis of *Homoeodictya.* Such species have previously comprised part of the genus *Esperiopsis.*

Isodictya deichmannae[9] (de Laubenfels) new comb.

SYNONYMY:

Esperiopsis quatsinoensis Lambe, 1893. (As used by Procter, 1933, p. 94)
Neosperiopsis deichmanni de Laubenfels, 1949, p. 15

DISCUSSION: De Laubenfels (1949) established a new genus and species for this sponge which occurs along the Atlantic Coast of North America from Block Island Sound to the Grand Banks off Newfoundland. For a generic character he pointed to the presence of "distinctive" microscleres which he considered as reduced chelas resembling "sigmas with forked ends." His figures of these microscleres are very crude and bear only a vague resemblance to the spicules observed by the present author in de Laubenfels' type specimen (MCZ #6910). The microscleres (fig. 12b) found in all fifteen specimens examined by the writer correspond to the description and excellent figures given by Lundbeck (1905) of the *"Homoeodictya"* type of chela. This chela has the axis extended outward so as to form a projection inside the tooth of each end. In side view immature forms of this microsclere might possibly be interpreted as being sigmas with forked

[9] De Laubenfels named this species in honor of Dr. Elisabeth Deichmann, but nevertheless used the masculine ending for the specific name, *"deichmanni."* This *lapsus calami* is corrected above in accordance with article 14c of the International Rules of Zoological Nomenclature.

ends; however, specimens viewed from the front give unmistakable evidence of the chelate form, as do completely formed specimens in either view. The microscleres characteristic of this species are unquestionably identical with those of the species *Isodictya palmata* (fig. 13b).

Indeed, this sponge bears a general resemblance to *Isodictya palmata* (Lamarck)[10] Bowerbank, so much so that it is frequently impossible to distinguish the two species on the basis of external characteristics alone (see Pl. 6, figs. 1 and 4). The only certain difference between them is the type of megasclere present. In one form, styles are present; in the other, oxeas. The similarities between the two species are as follows:

(1) In both species a reticulate skeletal framework exists consisting of primary spicule tracts held together by a spongin sheath and radiating out from the axis of the branches to the surface. Secondary fibers connect the primary tracts at irregular intervals. (See figures 14 and 15.)
(2) In both species the same variety of isochelate microscleres exist.
(3) The oscules in both species are distributed along the sides of the branches and are of similar diameters.
(4) The range of external shapes is similar in both species. (See Pl. 5, figs. 3, 4, 5, and Pl. 6, figs. 1–5.)

In spite of these many resemblances the two species have been placed in different genera by previous authors on the basis of the single criterion, megasclere shape. Table 11 indicates that the two species overlap in regard to this character. Specimens of *Isodictya palmata* from the Atlantic Coast of North America frequently possess a small number of styles in addition to oxeas[11] (fig. 13); specimens of the styliferous species often bear some oxeas (fig. 12). There seems to be little question but that these two species must be included in the same genus.

The question now arises as to whether the two forms belong to the same species. On the basis of geographical distribution this is unlikely. *Isodictya palmata* is a widely distributed boreal species which is known from northern England, Scotland, the Shetland Islands, the Orkneys (these records from Johnston, 1842, and Bowerbank, 1866); and from the Sea of Okhotsk (Burton, 1935). Along the Atlantic Coast of North America, it occurs off Nova Scotia and in the Gulf of Maine south to Eastport, Maine (Lambe, 1896; Hartman). The style-bearing form is restricted to the coast of North America from the Grand Banks to Block Island Sound, according to present records based on specimens in the Peabody Museum.

A related group of species occurs on the Pacific Coast of North America. These were described by Lambe (1893) as belonging to four distinct species of the genus *Esperiopsis: rigida, vancouverensis, quatsinoensis,* and *laxa.* From the descriptions, figures, and ranges given in Lambe's article it seems not unlikely that these four species represent growth forms of a single species. A reëxamination of Lambe's types will be necessary to clarify this point. Procter (1933) who identified the style-bearing *Isodictya* from Mt. Desert Island, Maine, as *Esperiopsis quatsinoensis* Lambe, has tabulated the skeletal dimensions of Lambe's *E. vancouverensis, quat-*

[10] Topsent (1933) regards Lamarck's *Spongia palmata* as equivalent to *Isodictya palmata.*

[11] Swartschewsky (1906) reports the presence of occasional styles in specimens of *I. palmata* from the White Sea.

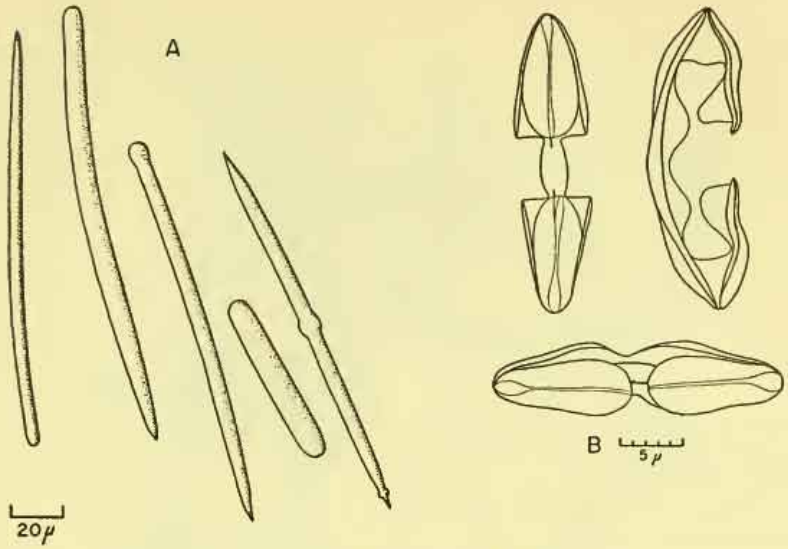


FIGURE 12. Spicules of *Isodictya deichmannae*. A Megascleres: styles, subtylostyle, strongyle, centrotylote oxea. B. Microscleres: isochelas in front (left and bottom) and side (right) views. Kent Isl., N. B. YPM #890.

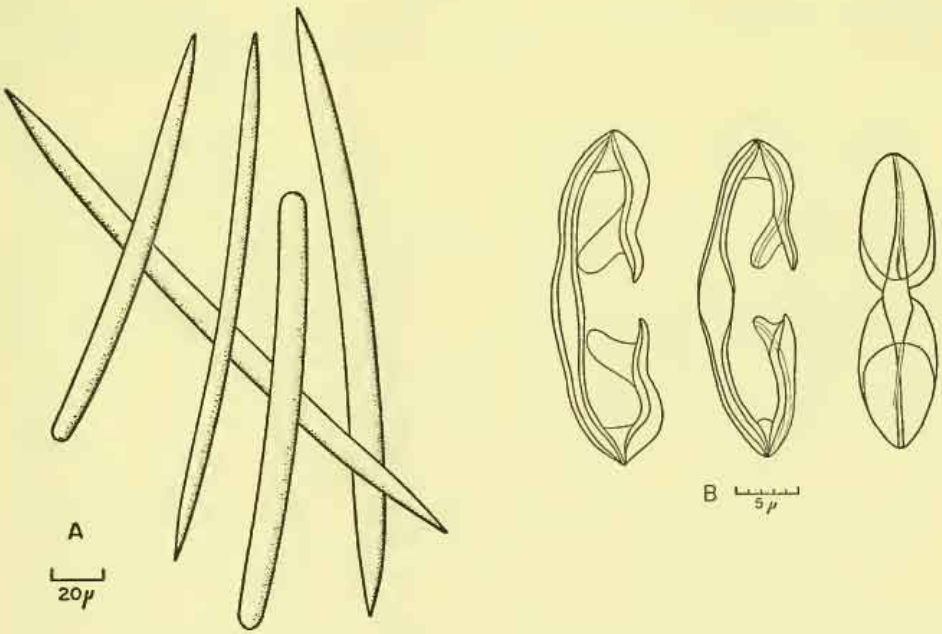


FIGURE 13. Spicules of *Isodictya palmata*. A Megascleres: oxeas, style, strongyle. B. Microscleres: isochelas in front and side views. Kent Isl., N. B. YPM #923.

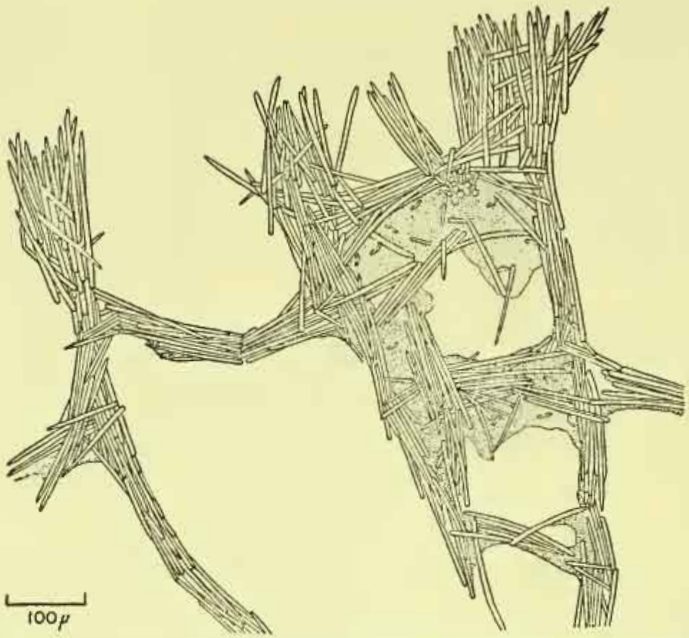


FIGURE 14. Portion of skeletal framework of *Isodictya deichmannae*. (Section perpendicular to surface.) Kent Isl., N. B. YPM #890.

sinoensis, and *laxa*. These three species intergrade in respect to these characters, and Procter concluded that they are synonymous. *E. rigida* differs in bearing two categories of styles in respect to width. This same variation occurs in some specimens of the East Coast species; these may represent specimens which were preserved at a time when active spicule-formation was taking place, the thin styles probably representing growth stages.

Procter's suggestion that the East and West Coast forms are identical is invalid in the present author's opinion. De Laubenfels' separation of the eastern and western species on the basis of megasclere width seems unjustified unless other characters can be found to differentiate them. More conspicuous characteristics separating the two species are the position and sizes of the oscules. All four of Lambe's species of *Esperiopsis* bear terminal oscules. Even *E. quatsinoensis*, which is described and figured with rows of oscules down the sides of the branches, also bears larger oscules at the tips of the branches. Two specimens of this species from St. Lawrence Island, Alaska (AMNH Nos. 264 and 267) were examined by the author. The colonies consist of clusters of branches each of which bears a large terminal oscule. No oscules are present along the side walls of the tubular branches. The oscules are elliptical or circular in outline and vary from 12 mm. x 7 mm. to 3 mm. x 3 mm. in diameter. On the other hand, all of the New England specimens studied by the present author lack terminal oscules and instead have the oscules arranged irregularly or in rows along the sides of the branches. The oscules in these specimens are circular and are much smaller, varying in diameter from 1 mm. to 3 mm.

De Laubenfels' species, *"deichmannae,"* is therefore a valid one, though not on the basis of the character suggested by him. The species is assigned to the genus

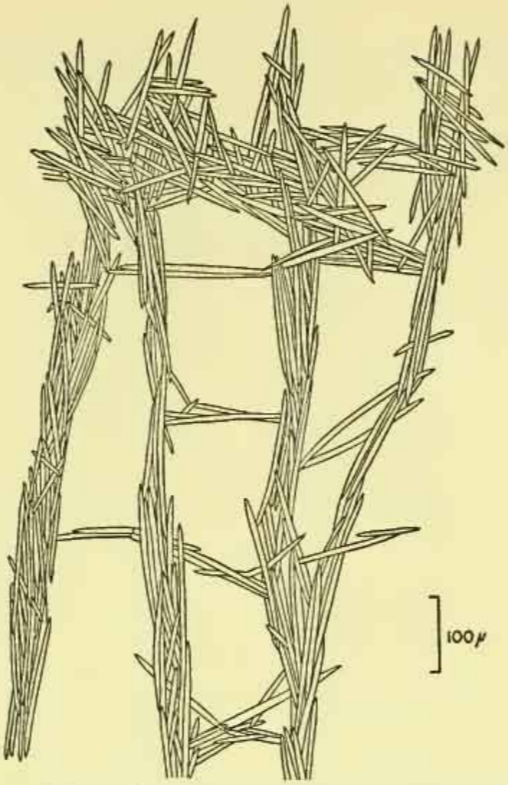


FIGURE 15. Portion of skeletal framework of *Isodictya palmata*. (Section perpendicular to surface.) Kent Isl., N. B. YPM #923.

Isodictya, being virtually indistinguishable from *I. palmata* except in regard to megasclere form.

It is of interest to note that microsclere form and size are remarkably constant in the three species studied here (see Table 13). On the other hand, the megascleres vary in length and width considerably; even their form is not constant in any one individual. A certain percentage of diactinal megascleres regularly occur along with the styles; small numbers of styles occur with oxeas. Hentschel (1929) has pointed out a number of trends in megasclere form correlated with temperature. Exotylote spiculation is an arctic phenomenon. Spicule size characteristically increases in colder waters. Oxeas often replace styles in waters with lower temperatures. The species pair under consideration here offers support for the two last mentioned trends.

Isodictya palmata appears to be a widespread subarctic species which has given rise to more southern species on both the East and West Coasts of North America. On the East Coast, at least, the northern and southern species overlap in part of their ranges.

DISTRIBUTION OF *Isodictya palmata* IN NORTH AMERICA: Nova Scotia to Eastport, Maine.

Nova Scotia and Sable Island (Lambe, 1896, p. 190); Minas Basin, Bay of

TABLE 13

SPICULE DIMENSIONS OF AMERICAN DESMACIDONIDS

LOCALITY CATALOGUE NUMBER	MEGASCLERES RANGE AND MEAN LENGTH AND WIDTH	CHELAS† RANGE AND MEAN LENGTH	PERCENTAGE OF OTHER MEGASCLERES	
Isodictya deichmannae				
	STYLES		OXEAS	STRONGYLES
Grand Banks YPM #419**	131–*196*–231μ x 9.5–*11.7*–14.3μ	25–*28*–33μ	—	0.5
Kent Island, N. B. YPM #890*	119–*180*–209μ x 5.3–*8.5*–11.9μ	18–*23*–31μ	—	5.0
Eastport, Maine YPM #152**	146–*191*–239μ x 5.1–*7.3*–12.1μ	21–*24*–33μ	3.5	—
Casco Bay, Maine YPM #446**	131–*182*–231μ x 6.2–*11.0*–15.4μ	21–*26*–33μ	6.5	0.5
Casco Bay, Maine YPM #2122*	119–*179*–201μ x 4.1–*9.9*–14.4μ	25–*29*–37μ	—	3.0
Georges Bank YPM #2123**	169–*234*–254μ x 5.5–*11.0*–13.9μ	25–*27*–32μ	1.0	—
Off Cape Cod YPM #2124**	139–*185*–316μ x 3.7–*7.7*–11.0μ	22–*26*–29μ	7.0	2.5
Nantucket Shoals YPM #2125*	119–*178*–205μ x 4.1–*8.8*–14.4μ	19–*21*–30μ	2.0	1.0
Off Nantucket YPM #2112*	144–*180*–205μ x 4.1–*10.3*–14.8μ	23–*26*–30μ	—	2.0
Off Nantucket YPM #2126*	103–*148*–185μ x 2.5–*6.4*–13.5μ	14–*19*–23μ	4.0	1.0
Off Nantucket YPM #2127*	119–*170*–209μ x 3.7–*7.5*–13.9μ	Microscleres rare; range of 6: 12–18μ	—	2.0
Off Nantucket YPM #2113*	98–*160*–197μ x 3.3–*10.2*–15.6μ	21–*25*–29μ	4.0	1.0
Woods Hole, Mass. YPM #2128*	113–*160*–179μ x 5.1–*7.0*–9.5μ	23–*26*–29μ	—	—

* Megasclere measurements based on 100 spicules per specimen.
** Megasclere measurements based on 200 spicules per specimen.
† Measurements based on 25 spicules per specimen.

(Continued)

TABLE 13—Concluded

SPICULE DIMENSIONS OF AMERICAN DESMACIDONIDS

LOCALITY CATALOGUE NUMBER	MEGASCLERES RANGE AND MEAN LENGTH AND WIDTH	CHELAS† RANGE AND MEAN LENGTH	PERCENTAGE OF OTHER MEGASCLERES	
Woods Hole, Mass. MCZ #6910*	123–*160*–185μ x 3.7–*6.7*–8.6μ	20–*26*–30μ	3.0	—
Block Isl. Sd. YPM #762*	119–*170*–197μ x 4.5–*8.1*–12.3μ	22–*28*–33μ	5.0	1.0
Block Isl. Sd. YPM #817**	108–*159*–216μ x 7.0–*8.4*–10.2μ	22–*25*–29μ	1.0	—
Noank, Conn. YPM #2129**	139–*182*–216μ x 5.5–*8.8*–12.1μ	21–*25*–29μ	—	—
Overall mean	177μ x 8.8μ	25μ	—	—

Isodictya palmata

	OXEAS	CHELAS	STYLES	STRONGYLES
Minas Basin, N. S. YPM #2114**	116–*177*–231μ x 5.5–*9.5*–13.9μ	23–*28*–33μ	0.5	—
Kent Isl., N. B. YPM #923**	169–*229*–277μ x 8.4–*11.3*–14.6μ	24–*26*–33μ	1.0	—
Eastport, Maine YPM #4**	162–*219*–262μ x 5.9–*10.2*–13.5μ	24–*28*–29μ	5.0	—
Eastport, Maine YPM #4A*	172–*216*–258μ x 4.5–*8.3*–16.0μ	23–*26*–29μ	1.0	—
Overall mean	210μ x 9.8μ	27μ	—	—

Esperiopsis quatsinoensis

	STYLES	CHELAS	OXEAS	STRONGYLES
St. Lawrence Isl., Alaska AMNH #264†	172–*192*–220μ x 7.7–*12.1*–15.7μ	24–*28*–35μ	—	—
St. Lawrence Isl., Alaska AMNH #267†	154–*190*–220μ x 9.2–*12.1*–14.6μ	22–*25*–29μ	—	—
Overall mean	191μ x 12.1μ	27μ	—	—

Fundy (Lambe, 1896, p. 190; Hartman—A. E. Verrill collections); off Kent Island, N.B. (Hartman); off Eastport, Me. (Hartman—A. E. Verrill collections).

DISTRIBUTION OF *Isodictya deichmannae* IN NORTH AMERICA: Grand Banks to Block Island Sound.

Grand Banks, exact locality unknown (Hartman—A. E. Verrill collections); off Kent Island, N.B. (Hartman); Eastport, Me. (Hartman—A. E. Verrill collections); Mount Desert Region, Me. (Procter, 1933, p. 94, as *Esperiopsis quatsinoensis*); Casco Bay (Hartman—A. E. Verrill collections); Georges Bank (Hartman—A. E. Verrill collections); Stellwagen Bank, Massachusetts Bay, 34 meters (Hartman); Vineyard Sound and Nantucket (Verrill *in:* Verrill and Smith, 1873, p. 742, as *Isodictya* sp.); Woods Hole, Mass. (de Laubenfels, 1949, p. 15, as *Neosperiopsis deichmanni*); Watch Hill, R. I. (Verrill *in:* Verrill and Smith, 1873, p. 742, as *Isodictya* sp.); Block Island Sound, 20–40 meters (Hartman); off Noank, Conn. (Hartman—A. E. Verrill collections).

It is impossible to say to which of the two species Sumner *et al.* (1913, p. 559) were referring as "*Desmacidon palmata* (Johnston)" since they mention no microscopic characters.

FAMILY HALICLONIDAE de Laubenfels

Haliclona oculata (Pallas, 1766) Grant,[12] 1841

SYNONYMY: See Lundbeck, 1902, p. 9 and Arndt, 1935, p. 100. To be included in the synonymy is *Chalina arbuscula* Verrill (*in:* Verrill and Smith, 1873, p. 742).

DISCUSSION: *Haliclona oculata* (Pallas) is a common sponge along the Atlantic Coast of North America from the Gulf of St. Lawrence to North Carolina. Verrill (*in:* Verrill and Smith, 1873) pointed out that specimens of this species occurring south of Cape Cod are "much more delicate, with more slender and rounder branches" than northern specimens.[13] He placed the southern forms in a new species, *Haliclona* (his *Chalina*) *arbuscula*. Since this species, although well described by Verrill (*op. cit.*) has given rise to some confusion in the literature, the present writer has undertaken to clarify its status. A biometric analysis has been made of specimens from a series of localities along the Atlantic Coast of North America from the Bay of Fundy to Long Island Sound. Mean dimensions of four characters (total height of colonies, mean width of branches at their bases [eight measurements per colony] and mean spicule length and width [50 measurements per colony]) are summarized in Tables 14, 15, 16. On the basis of these data, it is apparent that two morphologically distinct populations exist in the region under consideration, one occurring north of Cape Cod, the other, south of the Cape. The mean dimensions of each of the four characters for all localities considered collectively (1) to the north of and (2) to the south of Cape Cod, have been determined and are listed in Table 17. The means of three of the characters (total height, branch width, spicule length) differ significantly ($P<0.01$ in each case) when the northern and southern populations are compared, although the observed ranges overlap in all instances. The mean values of spicule width for the two populations are not significantly different, although the largest values for

[12] Grant spells the specific name as "*occulata*," but it is clear from his figure that he had this species in mind.

[13] Compare specimens from south of Cape Cod (Pl. 7, figs. 1, 2; Pl. 8, figs. 1, 2, 3; Pl. 9, fig. 5) with those occurring north of the Cape (Pl. 9, fig. 2; Pl. 10, figs. 1, 2, 3).

TABLE 14

VARIATIONS IN THE FORM OF *HALICLONA OCULATA* (PALLAS)

LOCALITY	NO. OF SPECIMENS MEASURED	RANGE AND MEAN HEIGHT OF COLONIES-MILLIMETERS	RANGE AND MEAN BRANCH WIDTH-MILLIMETERS*
Long Island Sound	14	100–*156*–190 (± 31)	3.1 x 2.1–*4.4* x *2.8*–7.1 x 3.7 (± 1.7, ± 0.8)
Block Island Sound	11	170–*267*–355 (± 59)	4.3 x 3.6–*5.4* x *3.6*–7.1 x 3.7 (± 1.6, ± 0.7)
Vineyard Sound	5	155–*199*–260 (± 34)	2.9 x 2.7–*4.4* x *3.1*–6.5 x 3.0 (± 1.8, ± 0.8)
Massachusetts Bay (Stellwagen Bank)	10	170–*267*–330 (± 48)	7.7 x 5.3–*9.3* x *5.3*–11.8 x 6.9 (± 2.7, ± 1.4)
Gulf of Maine	9	170–*277*–420 (±89)	5.2 x 3.8–*7.5* x *4.8*–9.9 x 4.6 (± 2.5, ± 1.1)
Georges Bank	1	290	9.0 x 3.5–*9.1* x *6.1*–13.5 x 7.0 (± 2.0, ± 1.5)
Atlantic Coast of N. A., South of Cape Cod	30	100–*207*–355 (± 44)	2.9 x 2.7–*4.7* x *3.2*–7.1 x 3.7 (± 1.7, ± 0.7)
Atlantic Coast of N. A., North of Cape Cod	20	170–*272*–420 (± 72)	5.2 x 3.8–*8.4* x *5.1*–13.5 x 7.0 (± 2.6, ± 1.3)
West Coast of Portugal (Arndt, 1941)	6	350	2.0–6.0
Channel Coast of France (St. Valéry-en-Caux)	2	170–*190*–210	3.6 x 3.1–*4.2* x *3.5*–4.8x3.8 (± 1.1, ± 0.8)
Hastings, Sussex, England (Bowerbank, 1874)	1	*ca.* 170	*ca.* 4.0–5.0
Faroes (Lundbeck, 1902)	2	39–*62*–85	.....

* Eight measurements per colony.

this character were observed in specimens from north of Cape Cod. If the four character means for colonies from each of the localities north of Cape Cod are compared with one another, there is no significant difference among them; the same is true for the localities south of Cape Cod (with the exception of total colony height in which there is a significant difference between the Long Island Sound and Block Island Sound populations).

Coefficients of difference (C. D.) for the four characters have been calculated, comparing values for all colonies north and south of Cape Cod (Mayr, Linsley, and Usinger, 1953); see Table 17. These data bear out Verrill's observations that the chief difference between the northern and southern populations is in branch size. In view of the extent of overlap in other characters, however, it seems unwarranted to separate the two populations into subspecies.

TABLE 15

SUMMARY OF VARIATIONS IN THE SPICULE SIZES OF *HALICLONA OCULATA* (PALLAS)

LOCALITY	NO. OF SPECIMENS MEASURED	MEAN SPICULE LENGTH AND RANGE–MICRONS	MEAN SPICULE WIDTH AND RANGE–MICRONS
Long Island Sound	6	84–*116*–156μ (±10.5)	3.7–*8.5*–12.8μ (±1.6)
Block Island Sound	4	84–*116*–139μ (± 8.0)	2.9–*7.7*–11.0μ (±1.3)
Newport, Rhode Island	1	88–*118*–132μ (± 7.9)	5.5–*9.2*–11.7μ (±1.4)
Vineyard Sound	3	77–*107*–137μ (± 9.6)	2.9–*6.2*–11.7μ (±1.2)
Atlantic Coast of N. A., South of Cape Cod	14	77–*114*–156μ (± 9.6)	2.9–*7.8*–12.8μ (±1.5)
Massachusetts Bay (Stellwagen Bank)	3	110–*137*–168μ (±10.9)	4.8–*9.7*–12.8μ (±1.3)
Casco Bay	5	108–*129*–156μ (± 8.1)	4.1–*7.8*–13.2μ (±1.3)
Bay of Fundy	2	103–*128*–165μ (±13.4)	7.3–*10.1*–12.8μ (±1.3)
Georges Bank	1	119–*141*–156μ (± 9.6)	5.7–*8.9*–11.5μ (±1.1)
Nantucket Shoals	1	127–*145*–168μ (±10.0)	5.7–*8.6*–11.5μ (±0.9)
Atlantic Coast of N. A., North of Cape Cod	12	103–*133*–168μ (±10.9)	4.1–*8.8*–13.2μ (±1.3)
West Coast of Portugal (Arndt, 1941)	6	83–103μ	8.0–10.0μ
Channel Coast of France (St. Valéry-en-Caux)	1	68–*97*–115μ	3.7– *4.8*– 5.5μ
Hastings, Sussex, England (Bowerbank, 1874)	1	*ca.* 119μ	*ca.* 9.4μ
Faroes (Lundbeck, 1902)	2	120–*149*–178μ	8.0–*11.0*–13.0μ

TABLE 16

SPICULE DIMENSIONS OF *HALICLONA OCULATA**

LOCALITY	SPICULE LENGTH RANGE AND MEAN	SPICULE WIDTH RANGE AND MEAN
New Haven, Conn. YPM #430	114–*123*–146μ	4.4–*9.5*–11.0μ
Mansfield Pt. (East Haven), Conn. YPM #810	84–*102*–121μ	4.8–*7.3*–10.6μ
Thimble Islands, Conn. YPM #469	88–*107*–124μ	5.9–*7.0*–8.1μ

* All measurements based on 50 spicules per specimen.

(Continued)

TABLE 16—Concluded

SPICULE DIMENSIONS OF *HALICLONA OCULATA**

LOCALITY	SPICULE LENGTH RANGE AND MEAN	SPICULE WIDTH RANGE AND MEAN
Hammonasset, Conn. YPM #820	92–*120*–156μ	3.7–*9.5*–12.8μ
Hammonasset, Conn. YPM #823	88–*120*–135μ	3.7–*9.2*–11.3μ
Noank, Conn. YPM #2130	90–*125*–152μ	4.8–*8.4*–11.7μ
Block Island Sound YPM #756	101–*116*–134μ	—
Block Island Sound YPM #757	95–*107*–117μ	3.3–*7.3*–9.9μ
Block Island Sound YPM #773	84–*116*–135μ	2.9–*7.0*–10.2μ
Block Island Sound YPM #780	112–*124*–139μ	7.3–*8.8*–11.0μ
Off Newport, R. I. YPM #2131	88–*118*–132μ	5.5–*9.2*–11.7μ
Woods Hole, Mass. MCZ #6908	79–*102*–115μ	2.9–*5.1*–6.6μ
Woods Hole, Mass. YPM #942	77–*103*–119μ	3.7–*5.5*–8.1μ
Vineyard Sound YPM #2132	97–*116*–137μ	5.1–*8.1*–11.7μ
Off Nantucket YPM #2137	127–*145*–168μ	5.7–*8.6*–11.5μ
Stellwagen Bank, Massachusetts Bay YPM #965A	110–*131*–156μ	5.5–*9.2*–12.4μ
Stellwagen Bank, Massachusetts Bay YPM #965B	110–*134*–163μ	4.8–*9.2*–12.1μ
Stellwagen Bank, Massachusetts Bay YPM #965C	115–*145*–168μ	7.3–*10.6*–12.8μ
Casco Bay, Maine YPM #448	108–*135*–150μ	5.9–*9.5*–13.2μ
Portland, Maine YPM #2116	115–*130*–144μ	5.3–*9.1*–12.3μ
Portland, Maine YPM #2133	111–*124*–156μ	4.9–*7.8*–12.3μ
Portland, Maine YPM #2135	111–*126*–152μ	4.9–*7.5*–10.7μ
Portland, Maine YPM #2136	115–*130*–144μ	4.1–*5.1*–8.6μ
Georges Bank YPM #2138	119–*141*–156μ	5.7–*8.9*–11.5μ
Kent Isl., N. B. YPM #924	110–*136*–165μ	7.3–*10.2*–11.0μ
Kent Isl., N. B. YPM #901	103–*120*–137μ	7.3–*9.9*–12.8μ

* All measurements based on 50 spicules per specimen.

TABLE 17

COEFFICIENTS OF DIFFERENCE FOR MEASUREMENTS OF *HALICLONA OCULATA* NORTH AND SOUTH OF CAPE COD

CHARACTER	MEANS AND S. D.		C. D.	PERCENT OF OVERLAP
	North of Cape Cod	*South of Cape Cod*		
Colony height	272mm. ±72	156mm. ± 31	1.126	87
Branch size*	44mm. ±13.0	15mm. ±5.7	1.545	94
Spicule length	133μ ±10.9	114μ ± 9.6	0.927	82
Spicule width	8.8μ ±1.3	7.8μ ± 1.5	0.361	75

* Product of the cross-sectional diameters.

The size differences between the northern and southern populations are clearly correlated with water temperature, and represent but another example of a common phenomenon, that of increase in size in northern, colder waters. Hentschel (1929) has pointed out a correlation of spicule length with water temperatures in several genera of siliceous sponges. His observations are given in Table 18.

Maximum and minimum surface and bottom temperatures for the regions under discussion are given in Table 19. The boundary between the northern and southern populations coincides with the summer cold-water barrier in the region of Cape Cod pointed out by Parr (1933). It is of interest to note that Vineyard Sound specimens agree well in size with those from farther south, whereas the one specimen available from Nantucket Shoals is close to the northern forms. Bigelow (1933) has pointed out the existence of a zone of upwelling in the latter area, which keeps the summer temperatures of Nantucket Shoals considerably colder than those just to the west.

Verrill (*in:* Verrill and Smith, 1873) recorded an overlap in range between *Haliclona* (*Chalina*) *oculata* and his *Haliclona arbuscula,* listing records of the

TABLE 18

SPICULE SIZES OF SILICEOUS SPONGES IN ARCTIC AND TROPICAL REGIONS

(From Hentschel, 1929)

GENUS	*POLYMASTIA*	*MYCALE*	*MYXILLA*	*GELLIUS*
SPICULE TYPES*	STYLES	STYLES	ACANTHOSTYLES	OXEAS
Arctic	1303	431	287	313
Tropical Regions of Atlantic	1140	365	157	264
Antarctic	1427	587	579	520

* Mean lengths of megascleres in microns.

TABLE 19

TEMPERATURE RANGES AT LOCALITIES WHERE *HALICLONA OCULATA* OCCURS

LOCALITY	SURFACE TEMPERATURE* MAXIMUM	SURFACE TEMPERATURE* MINIMUM	BOTTOM TEMPERATURE* MAXIMUM	BOTTOM TEMPERATURE* MINIMUM	AUTHOR
Long Island Sound	20.5–21	3.5	16-18.5 (30 meters)	1–3.5 (30 meters)	Fuglister, 1947 Riley, 1948
Block Island Sound	20.5–21	3.5	15.5–19 (20–30 meters)	3–5 (20–30 meters)	Fuglister, 1947 Riley, 1948
Vineyard Sound	20–20.5	3.5	15.5–20 (15–30 meters)	1–3 (15–30 meters)	Fuglister, 1947 Riley, 1948
Massachusetts Bay (Stellwagen Bank)	18–>20	2–2.5	11–12 (20–25 meters)	1–2 (20–25 meters)	Bigelow, 1928
Gulf of Maine (Casco Bay)	14.5–15	1–1.5	7–9 (30 meters)	1.5 (30 meters)	Bigelow, 1914, 1928
Georges Bank	15–18	3–4	6–10 (120 meters)	2.5–3.5 (120 meters)	Bigelow, 1928
Kent Island	10–11	1.5–2.0	9–10 (40 meters)	1.5–2.0 (40 meters)	Bigelow, 1928
Nantucket Shoals	12–16	2.5–4.5	12–14 (30–40 meters)	3–4 (30–40 meters)	Bigelow, 1933
Channel Coast of France (St. Valéry-en-Caux)	17–17.5	7–8	—	—	Hutchins and Scharff, 1947
Faroes	11.5–12	6–6.5	—	—	Hutchins and Scharff, 1947

* All temperatures recorded in degrees centigrade.

former from off Watch Hill, R. I., and off Gay Head, Martha's Vineyard. It is apparent from Table 14 that Block Island Sound specimens (see also Pl. 7, figs. 1, 2; Pl. 8, figs. 1, 3) are significantly taller than those from Long Island Sound (Pl. 8, fig. 2; Pl. 9, fig. 5) and in regard to this character resemble the northern populations. But in branch size and spicule dimensions, the Block Island Sound specimens agree with other populations south of Cape Cod. Verrill was probably misled by the large colony size when he regarded the Watch Hill specimens as being identical to forms from the Gulf of Maine.

The populations of *H. oculata* in Vineyard Sound and off the western end of Martha's Vineyard are distinctive in colony form and color. Verrill (*op. cit.*,

p. 497) describes specimens from off Gay Head as having flattened stalks which fork distally and divide into numerous digitate branches.[14] The color of these individuals is described as dull orange red when alive. Dr. Werner Bergmann has collected specimens identical with these in shallow water off Woods Hole, Massachusetts. One specimen of his collection available to the author (Pl. 9, fig. 4) shows the following spicule dimensions: length (range and mean), 76.9–*103.2*–119.0μ; width (range and mean), 3.7–*5.5*–8.1μ. The total height of this colony is 185 mm. and the mean branch width is 6.5 x 3.0 mm. This specimen thus fits into the southern population as far as the dimensions of the four characters listed above are concerned. It seems to differ from typical representatives of this population in two ways; (1) its palmate manner of branching with terminal branches arising from broad, flattened bases; (2) its orange-red color. The range of variation in form in this species is great. Some specimens from Block Island Sound and Long Island Sound show a similar tendency to a formation of palmate branches, and it is probable that all intermediates could be found between the typical mode of branching from the base of the sponge to the palmate condition. On the other hand, the orange-red color has never been observed by the present writer in any specimens of either the northern or southern populations. It is of interest that this distinctive color, observed by both Verrill and Bergmann in much the same region, should be associated in both cases with the extreme palmate branching habit.[15] It will be necessary to obtain a larger series of specimens from this region, as well as cytological information and data on breeding habits and larval characteristics, in order to determine the status of this population. For the time being it is regarded by the present writer as a variant population of *H. oculata,* close to, but not identical with, populations to the south.

It is of interest to note that, at least as far as the few observations and literature references available to the present author are concerned, a similar correlation of structural characteristics with temperature is present in *Haliclona oculata* in European waters. Spicule measurements of two specimens of *Haliclona oculata* from the Faroes, as reported by Lundbeck (1902), agree with those of the northern population of the western North Atlantic. On the other hand, specimens collected for the writer by French fishermen at St. Valéry-en-Caux, on the northern coast of France (Pl. 9, fig. 3), show colony and spicule dimensions comparable to those of the southern population of the North American Coast. (See Tables 14, 15.) A specimen figured by Bowerbank (1874, Pl. 66) and collected in the English Chan-

[14] Short colonies with a palmate pattern of branching (Pl. 9, fig. 1) were collected by Verrill off Nantucket. In some of these colonies the flattened basal portions break up into many thin branches distally, thus resembling the colonies described by Verrill from off Gay Head. More exact locality data for these colonies are not recorded, but they are probably from the relatively shallow waters of Nantucket Sound rather than from the Shoals to the south of the island. They bear a close resemblance externally to the Woods Hole and Vineyard Sound populations.

[15] Sumner *et al.* (1913, p. 558) report that Dr. J. A. Cushman was uncertain of the identity of the *"Chalinas"* in the Woods Hole area and preferred to enter all of them as "undetermined." De Laubenfels (1949, p. 32) suggests that Verrill's Vineyard Sound specimens of *Chalina arbuscula* may represent *Haliclona palmata* (Ellis and Solander); however, the colony height and spicule dimensions given by de Laubenfels for a specimen of *H. palmata* from Woods Hole are much smaller than those of Verrill's Woods Hole specimens of *Chalina arbuscula* (see Pl. 9, fig. 1A). Burton (1930a, p. 511) regards *Spongia palmata* Ellis and Solander as "clearly an uncommon form of *Chalina oculata* occasionally occurring on the British coasts."

nel off Hastings fits into the same group. The English Channel specimens, although resembling the more southern American population in having small spicule dimensions and branch width measurements, differ from the latter in a tendency for the oscules to be raised above the surface of the branches on small conules.

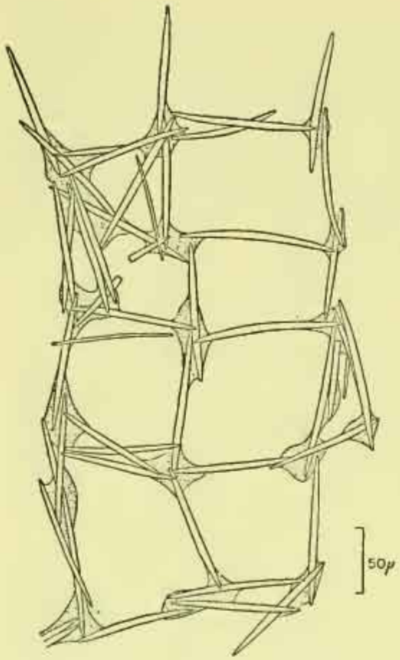
Specimens of *Haliclona oculata* from the west coast of Portugal have round branches; the spicules are somewhat shorter than those of either the southern population of the American Coast or the English Channel specimens. Arndt (1941) regarded the Portuguese population as a subspecies, *tavaresi*.

A word must be said about Fristedt's records of "*Chalina arbuscula* Verrill" from the southwest coast of Sweden (1885) and from northern Spitsbergen, northern Siberia, and the Bering Straits (1887). These records, which have been cited by Hentschel (1929) and Arndt (1935), if true, would invalidate the discussion of the zoogeography of *Haliclona oculata* presented here. Alander (1942) has concluded that the forms which Fristedt identified as "*Chalina arbuscula* Verrill" actually belong to several species including *Haliclona implexa* (Schmidt) and *Haliclona montagui* (Fleming). Apparently Fristedt's specimens are not synonymous with the species studied by Verrill in the western North Atlantic.

It is impossible to say at present whether the size differences observed between the northern and southern populations have a genetic or ecophenotypic basis. Transplantation experiments have so far proved impossible because of the difficulty of transplanting the northern specimens successfully to Long Island Sound. Experiments on the effect of temperature on spicule size and spongin content would be of interest. The sharp temperature break separating the two populations in the region of Cape Cod may isolate them reproductively, but definite evidence of this is lacking. Specimens from Block Island Sound bearing larvae were collected on July 23, 1944, but breeding colonies from north of Cape Cod have not been found as yet. It the Block Island Sound colony, eggs measure 53 x 40μ; embryos, from 230 x 230μ to 245 x 185μ.

NOTES ON MORPHOLOGY: Although Verrill's description (*in:* Verrill and Smith, 1873, pp. 742–43) of the southern population is adequate and the northern population is well-known from descriptions of northern European representatives of the species, several comments on the morphology of *Haliclona oculata* are worthy of mention. The amount of spongin associated with the skeleton varies greatly from specimen to specimen and shows no clear-cut correlation with geographical distribution. Figures 16, 17, and 18 illustrate the range in variation in the southern population. Here the skeletal framework consists of a rectangular network of single spicules and these are sometimes imbedded in continuous fibers of spongin, sometimes joined together at their tips only by small amounts of spongin. In the northern population (fig. 19) spongin fibers are the rule, with the main tracts bearing from two to four spicules per cross-section, and the connecting fibers usually containing single spicules. Mesh sizes vary with spicule length. The amount of spongin joining the spicules may vary in different parts of the same colony. Figure 20 illustrates different portions of a colony from the Channel Coast of France. In this case, there is a basic network of spicule-containing spongin fibers running through the branches, but between these fibers runs a secondary reticulation of spicules joined at their ends by small amounts of spongin. Solid fibers are more common in the interior of the branches.

In colonies from both the northern and southern American populations are found a few extensive longitudinal spongin fibers, almost or entirely devoid of



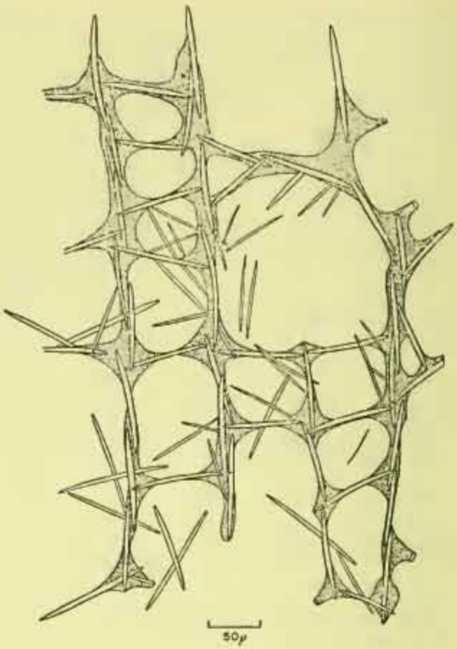


FIGURE 16. *Haliclona oculata.* Portion of skeleton (section perpendicular to surface) with small amount of spongin. Spongin stippled. Long Island Sound. YPM #2118.

FIGURE 17. *Haliclona oculata.* Portion of skeleton (section perpendicular to surface) with spongin tracts. Spongin stippled. Block Island Sound, 35 meters. YPM #757.

spicules. They are illustrated in a specimen from Long Island Sound (fig. 18). The regular network of spicules and spongin found through the sponge colony is joined to these occasional, sturdy spongin fibers which serve to give additional support to the skeleton.

Width measurements of the fibers in question for four specimens from north and south of Cape Cod are as follows: Long Island Sound (Off Mansfield Pt., Conn.), 25 to 50μ; Long Island Sound, 23–35μ; Casco Bay, 30–50μ; Bay of Fundy (off Kent Island, N.B.), 33–46μ. Heavy fibers of this type are not present in specimens from the Channel Coast of France.

Tracts of elongate cells in which spicules are aligned, similar to those described in *H. loosanoffi* and *canaliculata,* were noted in a specimen of *H. oculata* from Fipennies Ledge, Gulf of Maine.

The generally larger size of the northern individuals extends to the flagellated chambers. In a specimen from Fipennies Ledge, Gulf of Maine, these range from 36 x 26μ to 43 x 33μ. In a specimen from Block Island Sound, they range in size from 21 x 21μ to 26 x 20μ.

DISTRIBUTION IN NORTH AMERICA: Gulf of St. Lawrence to North Carolina.

River and Gulf of St. Lawrence (Lambe, 1900b, p. 155; Whiteaves, 1901, p. 15); coast of Nova Scotia (Lambe, 1896, p. 184; Whiteaves, 1901, p. 15); Minas

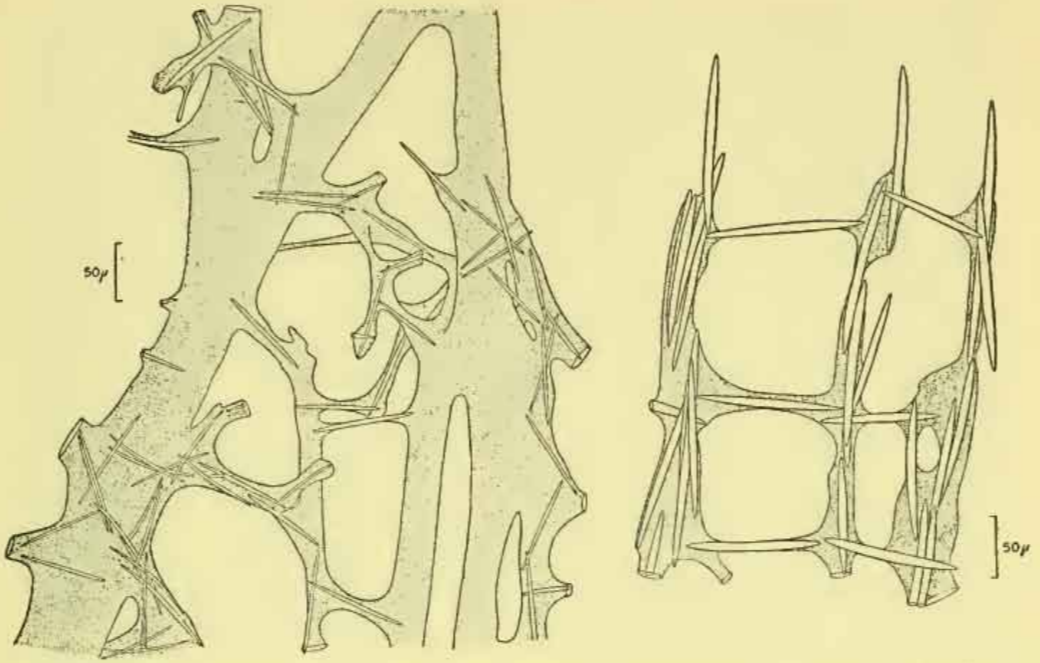


FIGURE 18. *Haliclona oculata.* Portion of skeleton in interior of branch, showing extensive development of spongin. Spongin stippled. Long Island Sound (off Mansfield Pt., East Haven, Conn.), 8 meters. YPM #810.

FIGURE 19. *Haliclona oculata.* Portion of skeleton (section perpendicular to surface) with spongin tracts. Spongin stippled. Fipennies Ledge, Gulf of Maine, 75 meters. YPM #995.

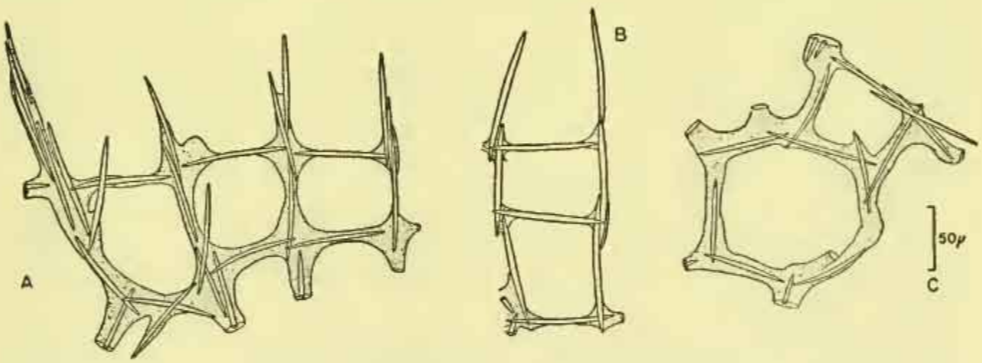


FIGURE 20. *Haliclona oculata.* Portions of skeleton from different parts of the same colony. Channel Coast of France (near St. Valéry-en-Caux). YPM #1073. A and B. Sections perpendicular to surface. C. Portion of skeleton from interior of colony.

Basin, Bay of Fundy (Lambe, 1900b, p. 155; Whiteaves, 1901, p. 15; Hartman—A. E. Verrill collections); Bay of Fundy, low water to 150 meters (Verrill, *in:* Verrill and Smith, 1873, p. 742); off Kent Isl., N. B., 30 meters (Hartman); Eastport, Me. (Hartman—A. E. Verrill collections); Mount Desert Region, Me. (Procter, 1933, p. 93); Casco Bay, Me. (Verrill, 1874a, p. 44, 1874b, p. 364, and 1880, p. 232; Kingsley, 1901, p. 161); Portland, Me., on wharf piles (Verrill, 1874a, p. 133); Fipennies Ledge, Gulf of Maine, 80 meters (Hartman); Stellwagen Bank, Massachusetts Bay, 40 meters (Hartman); Georges Bank (Smith and Harger, 1876, p. 22; Hartman—A. E. Verrill collections); off Gay Head, Martha's Vineyard, 8 to 30 meters (Verrill, *in:* Verrill and Smith, 1873, p. 742); Vineyard Sound, (Verrill, 1880, p. 232, as *Chalina oculata*); Vineyard Sound, 2 to 16 meters (Verrill, *in:* Verrill and Smith, 1873, p. 743, as *Chalina arbuscula*); Woods Hole, Mass. (Allee, 1923, p. 175, as *Chalina arbuscula;* de Laubenfels, 1949, p. 9; Hartman; see also the discussion by Sumner *et al.* 1913, p. 558); off Watch Hill, R. I. (Verrill, *in:* Verrill and Smith, 1873, p. 742; also reported as *Chalina arbuscula* on p. 743); Block Island Sound, 20–40 meters (Hartman); Long Island Sound, west to New Haven, to 10 meters (Hartman); off Long Island, N. Y. (Rafinesque, 1819, p. 150, as *Spongia cespitosa*); Great Egg Harbor, N. J. (Verrill, *in:* Verrill and Smith, 1873, p. 743, as *Chalina arbuscula*); Ft. Macon, N. C. (Coues and Yarrow, 1879, p. 312, as *C. arbuscula*); North Carolina (Verrill, *op. cit.*, p. 743, as *C. arbuscula*).

Haliclona loosanoffi sp. nov.

Shape and size of colonies: Connecticut colonies (Pl. 11) encrust rocks, shells, and algae, and range in size up to 15 cm. in diameter and 1.0 to 1.5 cm. in thickness. Vertical tubules are always present, varying in height from 2 to 33 mm., with basal diameters of 1 to 4 mm. The taller tubules often branch and anastomose with neighboring ones. Sometimes the tubules bifurcate or trifurcate distally. Maryland colonies (Pl. 12, figs. 2, 3) range up to 2 to 3 cm. in thickness, with short tubules (5 mm.) arising from the basal encrusting mass. The largest colony from the Maryland population measures 9 x 7 cm. in horizontal dimensions. Colonies with elongate branches are less frequent in the series from Maryland in the collections at Peabody Museum.

Color in life: Various shades of dark tan, gold, and drab (Maerz and Paul, 1950: Pl. 11, F-5; Pl. 12, D-4; Pl. 13, F-5, F-6, F-7, G-7, I-7; Pl. 14, G-5, G-6, G-7, H-6). Often the same colony will show gradations from a darker to a lighter color; one such colony, collected in August, varied from gold (Pl. 13, I-7) to beige (Pl. 12, D-4). The lighter colored portions of the colony seemed partially degenerate, possibly because of contact with mud beneath the rock on which the colony was growing. Some of the larger colonies are tinged with pink or lavender.

Consistency: Soft and compressible.

Surface: Sparsely hispid, resulting from the fact that multispicular tracts frequently penetrate the surface, thus raising the dermal membrane into small cones above the general surface of the colony. The surface tufts of spicules are from 250 to 600μ apart.

Oscules: Usually borne terminally on tubules; distributed as well along the sides of the taller tubules. Circular in outline, with diameters ranging from 1.0 to 2.4mm; or elliptical, with diameters ranging from 0.8 x 1.5mm. to 1.5 x 2.0mm. (preserved specimens).

Pores: Distributed singly or in groups. Usually elliptical in outline, ranging in diameters from 10 x 8μ to 25 x 20μ in preserved specimens.

Ectosomal anatomy (see fig. 21): The dermal membrane is thin and lacks spicules; it is made up of a layer of exopinacocytes beneath which are one or two layers of elongate amoebocytes. The dermal membrane is separated from the endosome by extensive subdermal cavities, continuous with the incurrent and excurrent channels. The dermis is supported by numerous mesenchymal trabeculae and vertical spicule tracts which traverse the subdermal cavities. Terminal spicules of the vertical tracts pierce the dermis at intervals of 250 to 600μ.

Endosomal anatomy (see fig. 21): The endosome consists of trabeculae of cells separated by the incurrent and excurrent canal systems. The flagellated chambers are grouped in the trabeculae around excurrent canals; the canal system is eurypylous. The flagellated chambers are ellipsoidal in shape, with diameters varying from 36 x 23μ to 26 x 21μ. The choanocyte cell bodies are 2.3 to 3.0μ in diameter; their nuclei are basal. The subdermal cavities as well as the canals of the aquiferous system are lined by endopinacocytes. Cell strands, 15 to 40μ in diameter and up to 850μ in length, run through the endosome at intervals. These strands are made up of numerous elongate cells containing basophilic granules and occasional round cells with eosinophilic granules. Such cell strands always have young spicules imbedded in them and may be compared to the "cordons cellulaires" described by Herlant-Meewis (1949) in *Spongilla*. As Herlant-Meewis has suggested, these cell strands doubtless serve as auxiliary supporting structures and also help to isolate and direct the spicules during their formation.

Skeleton: Multispicular tracts joined by spongin (2 to 6 spicules per cross-section) run vertically through the endosome, terminating in the dermal membrane (fig. 22). Horizontally placed individual spicules connect adjacent tracts at frequent intervals forming a loose network. The amount of spongin present varies greatly from colony to colony and even in different parts of a single colony, ranging from small amounts joining adjacent spicule ends to continuous fibers enclosing spicules. Burton (1926) observed a similar range of variation in the British haliclonid, *Reneira cinerea*.

The spicules are chiefly oxeas which taper gradually to sharp points and curve gently at the mid-point. Some specimens have small numbers of styles and (or) strongyles in addition to the oxeas (fig. 23). The oxeas vary greatly in size from specimen to specimen, the range of mean values for 21 specimens (based on 100 measurements for each specimen) is: length, 85 to 156μ; width, 4.0 to 7.2μ. The absolute ranges of spicule size for all 21 specimens are: length, 66 to 185μ; width, 2.0 to 8.2μ. Strongyles and styles are generally somewhat shorter than the mean lengths of oxeas in any specimen.

Gemmules: Characteristic of this species is the formation of gemmules during late summer (beginning in late August) and early fall. The gemmules form in a basal layer in contact with the substratum to which they remain attached after degeneration of the colonies (fig. 24; Pl. 12, figs. 1, 4). The gemmules are usually hemispherical in shape, flattened on the lower surface. Occasionally they are elongated into ellipsoidal or ovoid shapes. Dimensions of gemmules from Connecticut specimens: horizontal diameter, 315 to 515μ; height, 215 to 330μ. Gemmules of the Maryland colonies examined are larger, ranging in horizontal dimensions from 360 x 325μ to 1000 x 725μ.

In life the gemmules are white in color in Connecticut colonies and are difficult to detect on oyster or barnacle shells. The gemmules of Maryland colonies,

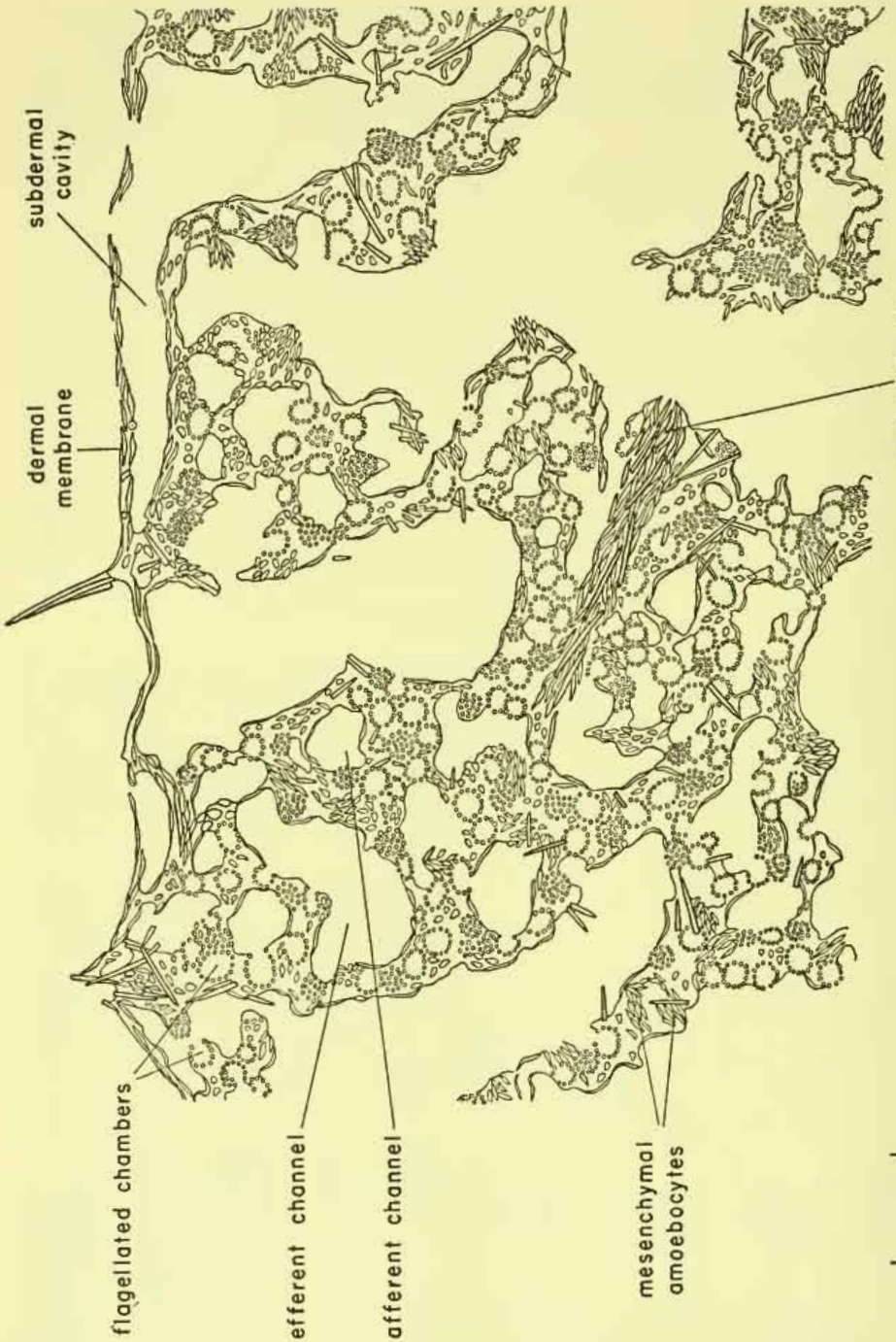


FIGURE 21. Anatomy of *Haliclona loosanoffi* (section perpendicular to surface). Hammonasset, Conn. YPM #1829C.

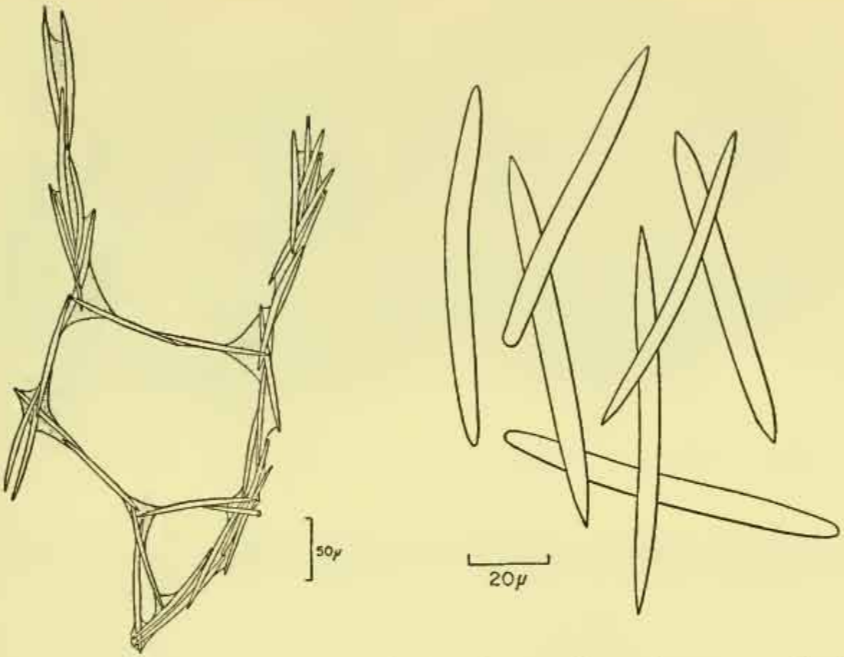


FIGURE 22. Portion of skeleton of *Haliclona loosanoffi* (section perpendicular to surface). Milford Harbor, Conn. YPM #859B.

FIGURE 23. Spicules of *Haliclona loosanoffi*. Oxeas, styles, strongyles. Pine Orchard (Branford), Conn. YPM #1833.

preserved in alcohol, are yellow. Each gemmule is enclosed in a spongin capsule in which special oxeas are imbedded. The base has relatively few spicules, however. The gemmule spicules are slightly shorter and wider than the skeletal spicules; they tend to be straight or only slightly curved. The range of mean spicule size of four specimens (25 measurements per specimen) is: length, 83 to 95μ; width, 4.1 to 6.3μ. Absolute range in size: length, 69 to 102μ; width, 3.3 to 6.9μ.

In early stages of formation, the gemmules consist of elongate cells, presumably archaeocytes, containing minute, sparsely distributed granules. It appears in sections that these cells migrate to the base of the colony from throughout the endosome. The engulfing of trophocytes by archaeocytes, as described by Leveaux (1939) in spongillids, was not observed. The basal layer of spongin is laid down first, and contains few spicules. Later, the entire mass of cells becomes enclosed in a spongin sheath in which oxeas are secreted (fig. 25). A layer of granule-free cells underlies the spongin sheath, and it is presumed that these secrete the spongin. In mature gemmules the granules of the interior cells have increased greatly in number and size (up to 2.5μ in diameter) and many appear to have broken out of the cells (possibly an artifact). Preliminary histochemical studies[16] of these reserve

[16] Periodic acid-Schiff test for polysaccharides, negative; Millon reaction for proteins, weakly positive; Sudan Black B test for lipids, positive. The granules stain black with iron haematoxylin and red with Mallory triple. All staining was done on Bouin-fixed material, preserved in 70 per cent alcohol for several years. Conclusive results must await further studies with fresh material.

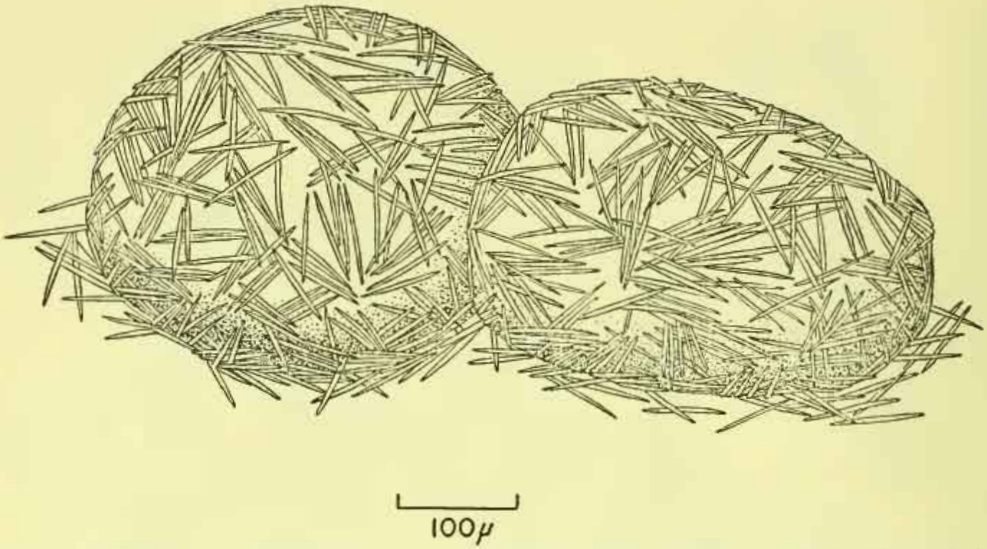


FIGURE 24. Gemmules of *Haliclona loosanoffi*. Milford Harbor, Conn. YPM #614.

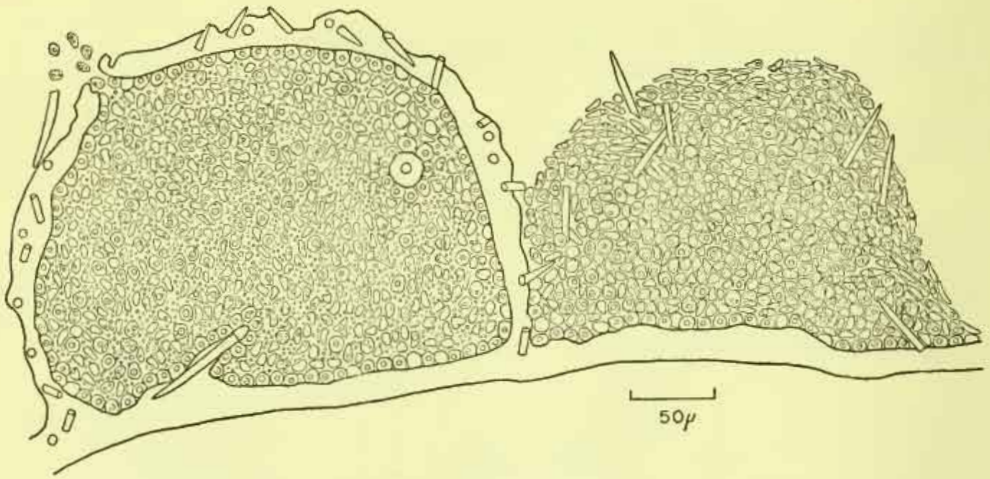


FIGURE 25. Cross-sections through gemmules of *Haliclona loosanoffi*. Left: mature gemmule covered by spicule-laden membrane of spongin. Right: Immature gemmule before formation of the spongin membrane. Pine Orchard (Branford), Conn. YPM #1832F.

granules suggest that they contain lipids and proteins, thus resembling the reserve substances in spongillids (Pourbaix, 1935).

EGGS AND EMBRYOS: Eggs and embryos were present in specimens collected in late August and early September. Eggs alone were found in colonies gathered in late September and early October. The eggs and embryos are located throughout the endosome in the cellular trabeculae. They appear in sections to occur in cavities, and the embryos are enclosed in limiting membranes (spongin?) adhering to

the outside of which is a layer of elongate cells. The cells of the embryos are filled with basophilic granules, presumably food reserves. Late stages of the embryos contain numerous thin oxeas arranged longitudinally throughout the interior. Dimensions: eggs, spherical to ovoid in shape, with diameters ranging from 25 x 25μ to 43 x 35μ; nuclear diameters, 8 to 15μ; nucleolar diameters, 3.5 to 5.0μ; embryos, subspherical to ellipsoidal in shape, with diameters ranging from 150 x 130μ to 215 x 185μ. The larval oxeas vary in size from 45 x 1.5μ to 55 x 1.5μ. Free-swimming larvae have not been found as yet.

HOLOTYPE: Yale Peabody Museum No. 614. Colony with gemmules collected below mean low water at Milford Harbor, Connecticut, in October, 1947.

REPOSITORIES OF OTHER TYPE MATERIAL: U. S. National Museum, Museum of Comparative Zoology, British Museum (Natural History). About 35 lots of specimens from six localities in central Connecticut and 12 lots from Solomons Isl., Maryland, were studied.

TYPE LOCALITY: Milford Harbor, Connecticut, from mean low water to a depth of two meters. Common as a fouling organism on submerged piles, floats, and shells.

FURTHER DISTRIBUTION: Long Island Sound to Maryland. This is a common sponge on the coast of central Connecticut, where it has been collected at Hammonasset State Park, Pine Orchard (Branford), Double Beach (Branford), Lighthouse Pt. (New Haven), and Bradley Pt. (West Haven), as well as at Milford. It usually encrusts the undersides of large rocks at and below mean low water level, occasional colonies occurring in tide pools up to mid-tide level. It is also a fouling organism on wharf piles, floats, and shells, chiefly in places not subject to direct sunlight. Several specimens have also been collected on oyster shells off Woodmont, Connecticut, at a depth of ten meters. Dr. I. M. Newell collected about 12 colonies of the sponge from wharf pilings at Solomons Island, Maryland. A similar sponge was found growing under the rocks of a breakwater at Stone Harbor, N. J. by the writer but the colonies lack the diagnostic gemmules, and their identity is still uncertain.

The numbers of this sponge show large annual fluctuations in some localities. In 1947 and 1948, it was a common fouling organism at Milford; in 1953 and 1954 not a single colony was found at this locality. In 1953 it was abundant at Hammonasset State Park; in 1954 only a few colonies could be found there. Nevertheless, the sponge was found in abundance at Pine Orchard in 1953 and at Double Beach in 1954, indicating that the population decline was not general in the region.

VARIATION: During the course of the studies of this species, great variations were noted in spicule size, and it seemed of interest to determine whether this character is correlated with geographic range and whether several sibling species might be present. Spicule slides of samples of 22 colonies from five localities were prepared, and length and width measurements were made of 100 spicules on each slide. The samples used for preparing the slides were about 0.5 cm^3 in size and were chosen to include all levels of the sponge. The data are given in Table 21.

The coefficient of variability of the mean values for spicule length of the 22 colonies is very high (C.V.=16.8), suggesting that the samples are not homogeneous. If the coefficient of variability of samples from each of the five localities is considered separately, those of Hammonasset and Double Beach are seen to be especially high (Table 20).

These data suggest the possibility that two sibling species of *Haliclona* are

TABLE 20

COEFFICIENT OF VARIABILITY OF SPICULE SIZE IN *HALICLONA LOOSANOFFI*

LOCALITY	NO. OF COLONIES	MEAN SPICULE LENGTH	C. V.
Hammonasset	8	104 ± 16.2	15.6
Double Beach	5	127 ± 18.4	14.5
Milford	4	100 ± 4.3	4.3
Pine Orchard	4	96 ± 8.0	8.3
Lighthouse Pt.	1	97	Insufficient data
First two localities	13	113 ± 20.4	18.1
Last three localities	9	98 ± 6.4	6.5
ALL LOCALITIES	22	107 ± 17.8	16.8

present on the Connecticut coast, one, with shorter spicules being found at all localities listed, the other with longer spicules, occurring along with the former at Double Beach and Hammonasset. If the mean spicule lengths of the Hammonasset and Double Beach colonies are compared with those of Milford, Lighthouse Point, and Pine Orchard colonies considered together, P=slightly>0.05, very near the borderline of significance.

If two species with differing spicule dimensions are actually present in the Hammonasset and Double Beach populations, other characters would be expected to show a correlation with spicule size. Such has not been found to be the case, so far. Tubule height and the occurrence of gemmules, e.g., show no correlation with spicule size. On the basis of present evidence, the several populations of *Haliclona loosanoffi* may be considered as representatives of a single species, highly variable in respect to spicule size and colony form.

OTHER SPECIES TO BE COMPARED WITH *Haliclona loosanoffi*: Encrusting haliclonids are notoriously difficult to define on the species level. They are often highly variable in regard to external form, skeletal characteristics, and color, so that these characters are reliable only if large samples of a population are studied. In the past many species have been described on the basis of one or two specimens, thus complicating the question of synonymy in the genus. The validity of the new species, *Haliclona loosanoffi*, is based most firmly on the occurrence of gemmules, although spicule dimensions and color also assume a significance when large samples are considered. It is probable that studies of larvae will also be important in distinguishing haliclonids when enough is known about them, just as they have been useful in the difficult genera, *Halichondria* (Topsent, 1911) and *Halisarca* (Lévi, 1953a, 1956).

Haliclona loosanoffi is superficially similar to *H. permollis* (Bowerbank), a

TABLE 21

SPICULE DIMENSIONS OF *HALICLONA LOOSANOFFI**

LOCALITY AND YPM CATALOGUE NUMBER	SPICULE LENGTH RANGE AND MEAN	SPICULE WIDTH RANGE AND MEAN	REMARKS
Hammonasset, Conn. No. 1821	76–*120*–149μ	2.3–*5.0*–7.3μ	Style: 102 x 4μ
Hammonasset, Conn. No. 1823	119–*138*–152μ	4.1–*5.9*–7.8μ	
Hammonasset, Conn. No. 1825	78–*88*–98μ	3.7–*4.4*–6.2μ	
Hammonasset, Conn. No. 1826	70–*91*–107μ	3.7–*4.2*–4.9μ	
Hammonasset, Conn. No. 850	82–*106*–131μ	4.1–*6.1*–8.2μ	Styles: 86–111μ x 4.9–8.2μ Strongyles: 94–111μ x 6.2–8.2μ
Hammonasset, Conn. No. 1822	90–*104*–115μ	3.3–*4.3*–5.3μ	
Hammonasset, Conn. No. 1824	82–*93*–103μ	2.1–*4.0*–4.5μ	
Hammonasset, Conn. No. 1829	70–*92*–111μ	2.9–*4.2*–4.9μ	
Pine Orchard (Branford), Conn. No. 1832	69–*85*–96μ	3.3–*6.1*–7.3μ	Style: 83 x 6.9μ Strongyle: 63 x 7.3μ
Pine Orchard (Branford), Conn. No. 1833	70–*100*–115μ	3.3–*5.6*–8.2μ	Strongyles: 94–107μ x 6.2–8.2μ
Pine Orchard (Branford), Conn. No. 1834	78–*92*–103μ	3.7–*5.9*–8.2μ	Strongyle: 70 x 5.3μ
Pine Orchard (Branford), Conn. No. 827	94–*106*–115μ	4.1–*7.2*–8.2μ	

* All measurements based on 100 spicules per specimen.

(Continued)

cosmopolitan species according to de Laubenfels (1936, 1949, etc.). The mean spicule dimensions given by the latter author (1949, see Table 22) are considerably larger than those of the Connecticut population. However, the spicule lengths given by Bowerbank in his description (1866) and illustration (1874) of the type

TABLE 21—Concluded

SPICULE DIMENSIONS OF *HALICLONA LOOSANOFFI**

LOCALITY AND YPM CATALOGUE NUMBER	SPICULE LENGTH RANGE AND MEAN	SPICULE WIDTH RANGE AND MEAN	REMARKS
Double Beach (Branford), Conn. No. 1838	83–*133*–152μ	2.0–*5.0*–6.6μ	
Double Beach (Branford), Conn. No. 1848	96–*131*–158μ	3.3–*5.8*–6.9μ	Styles: 119–219μ x 5.0–6.3μ
Double Beach (Branford), Conn. No. 1956 D–1	103–*156*–185μ	4.1–*5.6*–7.0μ	
Double Beach (Branford), Conn. No. 1956 E–1	86–*112*–144μ	4.1–*5.8*–7.8μ	
Double Beach (Branford), Conn. No. 1956 E–2	86–*103*–152μ	4.1–*5.9*–7.8μ	
Lighthouse Point, New Haven, Conn. No. 841	66–*97*–112μ	2.3–*6.0*–7.3μ	Styles: 89–99μ x 5.9–6.6μ
Milford Harbor, Connecticut No. 859	73–*101*–116μ	2.6–*5.3*–6.6μ	
Milford Harbor, Connecticut No. 614	90–*103*–115μ	4.1–*7.1*–8.2μ	
Milford Harbor, Connecticut No. 2139	90–*104*–115μ	2.1–*4.7*–6.6μ	
Milford Harbor, Connecticut No. 1876	78–*93*–107μ	2.5–*3.8*–4.5μ	
Solomons Isl., Md. No. 623	78–*104*–119μ	2.9–*6.3*–7.8μ	
Solomons Isl., Md. No. 627	90–*111*–127μ	4.1–*6.2*–8.2μ	

* All measurements based on 100 spicules per specimen.

are comparable to those of the Connecticut forms. De Laubenfels (1949) describes the color of living colonies of *H. permollis* as "a very distinctive lavender"; dead or "pathological" specimens are "dull, pale brown." Lavender-tinged specimens of *H. loosanoffi* are the exception, most colonies being tan to golden brown, in Connecticut, at least. In skeletal architecture the two species are very similar. However, gemmules have not been reported from *H. permollis;* it seems unlikely that they would have been overlooked by all of the many authors who have stud-

ied this species. The present author concludes that *H. loosanoffi* may be distinguished from *H. permollis* as a gemmuliferous species with smaller spicules and color differences.

Another species to be compared with *H. loosanoffi* is *Reniera tubifera* George and Wilson (1919), found at Beaufort, N.C. De Laubenfels (1947) considered this species as a synonym of *Haliclona permollis,* but in so doing he overlooked two important characters mentioned by George and Wilson concerning the consistency and dermal structure of their species. These authors state that *Reniera tubifera* is "not soft, but quite fragile," and they describe and figure "a distinct unispicular reticulum" in the dermis. The present writer has studied a series of haliclonid-like sponges collected at Beaufort Harbor, N.C., by Dr. Irwin M. Newell for the Peabody Museum. It is immediately apparent from consistency alone that two species are present in the series. One is soft and compressible; the other is "not soft, but quite fragile." Indeed, the colonies of the latter species, preserved in alcohol, have broken into many pieces just through handling of their container. The spicules of the first species are small; those of the second, large (see Table 22). The dermis of the first lacks spicules; that of the second is provided with "a distinct unispicular reticulum." There is no question that the second species in Newell's collection is *Reniera tubifera,* but the dermal spiculation suggests that it is not a *Haliclona* but rather a member of the genus *Adocia,* following the concept of that genus discussed by Burton (1934) and de Laubenfels (1936). The first-mentioned species is clearly a *Haliclona;* although it agrees with *H. loosanoffi* in spicule size and skeletal arrangement, further study is needed to identify it specifically.

Several other haliclonids recorded from the Atlantic Coast of North America may be compared with *H. loosanoffi. Reniera mollis* Lambe, 1893, recorded by its author from Labrador and the Baie des Chaleurs (1896), from Hudson Bay (1900a), and from Davis Strait and Hudson Strait (1900b) is an offshore species with large spicules and pores and is massive to lobate in form. *Reniera heterofibrosa* Lundbeck, 1902, recorded by Procter (1933) from the Mt. Desert region, Maine, has large spicules arranged in an irregular manner, resembling *Halichondria. Haliclona palmata* (Ellis and Solander, 1786) described by de Laubenfels (1949) from Woods Hole, has very small spicules enclosed in prominent spongin fibers.

Tubule-bearing colonies (Pl. 11, figs. 12 through 16) of *Haliclona loosanoffi* show a striking resemblance to the European species, *Halichondria montaguii* Fleming, 1828, as figured by Johnston (1842, Pl. 6, fig. 1). Other colonies (Pl. 11, figs. 8, 9, 10) resemble figures of *Chalina montaguii* (Bowerbank, 1866) and *Chalina flemingii* Bowerbank, 1866, given by Bowerbank (1874, Pl. 68, figs. 1–5). American specimens fit the descriptions given by these authors based largely on external form, color, and skeletal characteristics. Spicule dimensions recorded by Bowerbank for *montaguii* and *flemingii* (based on two spicules in each case) fall largely within the range of spicule sizes observed in *Haliclona loosanoffi.* Unfortunately it has not been possible to study Bowerbank's type material nor to obtain fresh material from England. That the American species is distinct from the British ones is supported by the disjunct pattern of distribution. It is unlikely that *Haliclona loosanoffi* occurs north of Cape Cod as would be expected in the case of a species occurring on both the British and American coasts. The author has made a thorough survey of the intertidal sponge fauna at six localities north of Cape Cod (Cape Ann, Mass.; Kittery, Maine; Cape Elizabeth, Maine; Boothbay

TABLE 22

COMPARISON OF AMERICAN AND BRITISH HALICLONIDS

SPECIES AND LOCALITY	AUTHOR	SPICULE DIMENSIONS	REMARKS
Haliclona loosanoffi Connecticut to Maryland	Hartman	Connecticut: 66–*107*–185μ x 2.0–*5.4*–8.2μ Maryland: 78–*108*–127μ x 2.9–*6.3*–8.2μ	Pores: 10 x 8μ to 25 x 20μ Oscules: 1.0 to 2.4 mm.
Haliclona sp. New Jersey	Hartman	111–*152*–180μ x 2.9–*5.5*–7.8μ	
Haliclona sp. Beaufort, N. C.	Hartman	78–*99*–119μ x 2.1–*4.9*–7.4μ	
Haliclona permollis Woods Hole	de Laubenfels, 1949	130–*150*–170μ x 6–*7*–8μ	Oscules: 1 to 5 mm.
Haliclona palmata Woods Hole	de Laubenfels, 1949	55–60μ x 2–3μ	Oscules: 1 to 3 mm. Fibers: up to 40μ
Reniera heterofibrosa Mt. Desert Region, Maine	Procter, 1933	121–*162* (mode) –203μ	
Reniera mollis Northeastern Canada	Lambe, 1896	170–299μ x 6–9μ	Pores: 65μ Oscules: 5 mm.
Isodictya permollis Great Britain	Bowerbank, 1866; 1874	113μ; 116μ	
Chalina montaguii Great Britain	Bowerbank, 1866; 1874	116μ x 8.5μ 127μ x 6.6μ	
Chalina flemingii Great Britain	Bowerbank, 1866; 1874	85μ x 3.4μ 102μ x 3.8μ	
Reniera tubifera Beaufort, N. C.	George and Wilson, 1919	125–170μ x 3–8μ	Pores: 50μ Fibers: 30–100μ
Adocia tubifera Beaufort, N. C.	Hartman	131–*159*–176μ x 2.9–*7.4*–9.0μ	

Harbor, Maine; Rockland, Maine; and Kent Island, N. B.) and has not found this haliclonid.

The species is named in honor of Dr. Victor L. Loosanoff, Director of the Biological Laboratory of the U. S. Fish and Wildlife Service, Milford, Connecticut.

Haliclona canaliculata sp. nov.

SHAPE AND SIZE OF COLONIES: The colonies form thin encrustations on rocks, shells, and algal holdfasts, ranging in size up to 10 cm. in diameter and from 2 to 8 mm. high (Pl. 15, fig. 1).

COLOR IN LIFE: Winter specimens: various shades of light buff, maple, and light tan (Maerz and Paul, 1950: Pl. 11, D-4, G-6; Pl. 12, B-4, C-6, D-5; Pl. 13, D-6). Summer specimens: dark tan to brown, drab, and gold. (Pl. 12, B-4; Pl. 13, D-5, E-4, F-7; Pl. 14, D-5, E-4, I-7).

CONSISTENCY: Moderately soft.

SURFACE: The surface of the colonies is raised at intervals into pointed, rounded, or ridge-like projections, 1-3 mm. high, where spicule tracts and cellular trabeculae traverse the subdermal cavities and reach the dermal membrane, pushing it above the general surface of the colony. Radiating subdermal excurrent channels converge upon the oscules and provide the surface with stellate patterns. These channels are often separated and rendered more prominent to the naked eye by ridges of choanosome which rise above the general surface of the colony. The circular openings of the incurrent channels leading from the subdermal cavities into the choanosome can readily be seen through the dermis by the unaided eye; these openings give the colony a punctate appearance (Pl. 5, fig. 2).

OSCULES: Circular or elliptical in outline, ranging in diameter from 0.8 x 0.6 mm. to 1.8 x 1.4 mm. in preserved specimens. The oscules are not elevated above the general surface of the colony as a rule; occasionally they are located on the summits of low mounds.

PORES: Occurring in groups above subdermal cavities, elliptical in shape, ranging in diameter from 30 x 16μ to 57 x 50μ.

ECTOSOMAL ANATOMY: The thin dermal membrane is composed of a layer of exopinacocytes underlain by one or two layers of elongate amoebocytes. The groups of dermal pores open into extensive subdermal cavities which in turn lead into wide incurrent canals. The openings into the latter from the subdermal cavities are readily apparent through the thin dermal membrane and appear to the naked eye like pores in the surface of the colony as noted above. Thin trabeculae of mesenchyme as well as occasional spicule tracts run through the subdermal cavities to the dermis, the spicules piercing the surface at intervals.

ENDOSOMAL ANATOMY: The endosomal mesenchyme consists of membranes or trabeculae of cells bounded by the extensive system of incurrent and excurrent canals. The canal system is eurypylous, the flagellated chambers opening directly into the excurrent canals. The flagellated chambers are ellipsoidal in shape, with diameters varying from 25 x 20μ to 35 x 25μ. The choanocytes range in diameter from 3.0 to 4.0μ. The excurrent canals of the endosome open into wide subdermal cavities which lead to the oscules. Both incurrent and excurrent canals are lined with endopinacocytes.

As in *Haliclona loosanoffi*, strands of elongate amoebocytes are frequent in the endosome. Tracts of spicules, free from spongin, lie in these cell strands which are 45 to 90μ in width and run chiefly parallel to the surface of the colony.

SKELETON: The basic framework of the skeleton consists of vertical multispicular tracts (three to ten spicules per cross section) held together by small quantities of spongin. The vertical tracts are joined by horizontally placed individual spicules or short tracts; in addition there are many irregularly arranged spicules between the tracts (fig. 26).

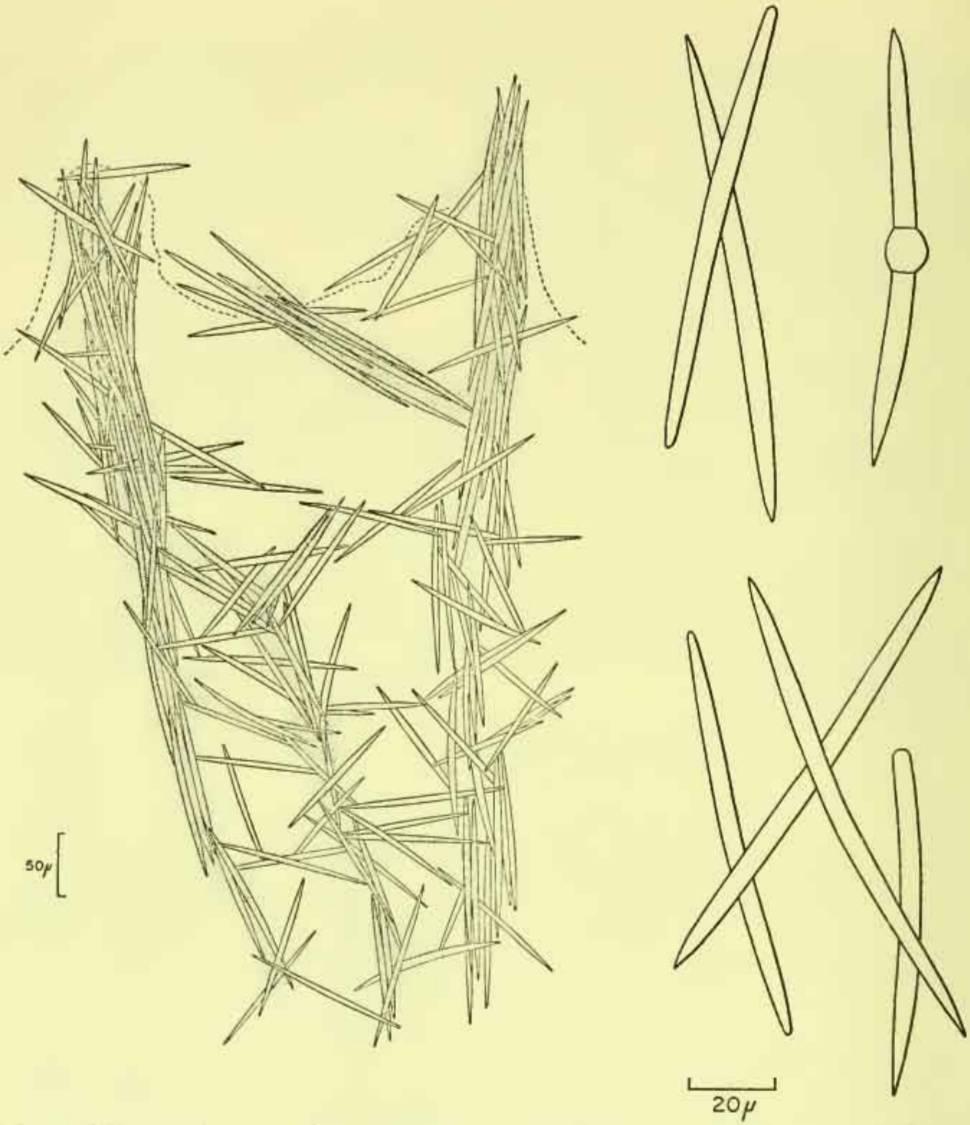


FIGURE 26. Portion of skeleton of *Haliclona canaliculata* (section perpendicular to surface). Spongin stippled. Dermis shown as dashed line. Double Beach (Branford), Conn. YPM #2016B.

FIGURE 27. Spicules of *Haliclona canaliculata*. Oxeas, styles, strongyles, centrotylote oxea on right. Double Beach (Branford), Conn. YPM #1955D.

Long horizontal multispicular tracts are also characteristic of this species; these are free of spongin but are associated with strands of cells as described above. Such tracts have been traced for distances up to 3mm. in sections perpendicular to the surface; they are about 75μ thick.

The spicules are oxeas, straight or gently curved in the middle, tapering gradually to sharp points (fig. 27). In some cases there is a step-wise reduction in width

TABLE 23

SPICULE DIMENSIONS OF *HALICLONA CANALICULATA**

LOCALITY AND YPM CAT. NO.	DATE OF COLLECTIONS	RANGE AND MEAN OF SPICULE LENGTH X WIDTH	REMARKS
Hammonasset 1827	August	86–*102*–115μ x 3.3–*4.3*–6.2μ	
Double Beach 1955D	September	107–*125*–139μ x 4.1–*5.9*–7.4μ	
Double Beach 1955E–1	September	98–*125*–148μ x 4.5–*6.7*–7.8μ	
Double Beach 1955E–2	September	94–*113*–123μ x 4.1–*5.3*–7.0μ	
Hammonasset 854	October	82–*112*–135μ x 3.7–*6.1*–8.2μ	
Double Beach 1785	January	103–*116*–131μ x 4.1–*7.9*–8.2μ	
Double Beach 1788	January	103–*122*–135μ x 5.3–*6.9*–8.2μ	Strongyles: 78–107μ x 5.3–8.2μ
Double Beach 1791	January	94–*112*–127μ x 5.3–*7.0*–8.2μ	
Double Beach 1803	February	74–*109*–131μ x 5.3–*7.7*–8.2μ	
Double Beach 1811	February	98–*113*–127μ x 4.5–*7.2*–8.2μ	
Double Beach 1813	February	94–*119*–131μ x 4.1–*5.7*–8.2μ	
Double Beach 1816	February	98–*113*–123μ x 5.3–*7.4*–8.2μ	Styles: 103–107μ x 5.3–6.1μ
Double Beach 1874	March	98–*118*–135μ x 4.9–*7.8*–8.2μ	
All summer specimens (5)	August to October	82–*115*–148μ x 3.3–*5.7*–8.2μ	
All winter specimens (8)	January to March	74–*115*–135μ x 4.1–*7.2*–8.2μ	

* All measurements based on 100 spicules per specimen.

at the ends. Styles and strongyles in small numbers are found in many specimens along with the dominant oxeas. There is less variation in the lengths of spicules than was observed in *Haliclona loosanoffi*. The range of mean spicule sizes for 13 specimens (based on 100 measurements per specimen) is 102 to 125μ in length and 4.3 to 7.9μ in width. The absolute range in length is 74 to 148μ; in width, 3.3 to 8.2μ. Styles and strongyles are shorter than oxeas. The coefficient of variation in spicule length is 5.8; in width, 16.7.

HOLOTYPE: YPM No. 2017. Collected on the underside of a rock, 0.5 feet below mean low water; Double Beach (Branford), Connecticut, Sept. 17, 1955.

REPOSITORIES OF OTHER TYPE MATERIAL: U. S. National Museum; Museum of Comparative Zoology, Harvard; and British Museum (Natural History). About 20 lots were studied.

TYPE LOCALITY: Double Beach (Branford), Conn. Common under rocks at mean low water and below.

FURTHER DISTRIBUTION: Two specimens were collected at Hammonasset State Park (Meig's Point), Connecticut.

DISCUSSION: *Haliclona canaliculata* differs from the other common encrusting haliclonid of Long Island Sound, *H. loosanoffi*, in being a perennial species. Colonies undergo some degeneration with the onset of cold weather, but portions of each colony remain alive throughout the winter months. These colonies show several differences from summer colonies: (1) they lack choanocytes, the endosome consisting of aggregates of amoebocytes (2) they possess thicker spicules. A more detailed investigation of the morphology and feeding habits of winter colonies is in progress. The occurrence of thicker spicules in winter colonies may reflect the greater availability of silicates during the winter, a fact observed in many hydrographic studies (Sverdrup, Johnson, and Fleming, 1946). This suggestion is supported by the experimental work of Jørgensen (1944) who found that the thickness (but not the length) of the microscleres of *Spongilla lacustris* increases with increasing silica content of the medium.

COMPARISON WITH OTHER SPECIES: In external form this species differs from other encrusting haliclonids of the American coast in the absence of branches and raised oscules. Conspicuous features of living and well-preserved colonies are the subdermal excurrent channels which appear to radiate out from the oscula, and the openings from the subdermal incurrent cavities into the incurrent endosomal canals which look like pores in the surface of the colony. The spicules are smaller than those of most other encrusting haliclonids (see Tables 22 and 23) of the American coast, except *Haliclona loosanoffi*, from which it differs in external shape and in lacking gemmules.

Reniera plana Topsent (1892) is a flat encrusting haliclonid, warranting comparison with *H. canaliculata*. The Mediterranean sponge has its spicules arranged in a unispicular network, however, and the spicules are much larger (235–250μ x 9μ) than those of the species described herein.

SUMMARY

1. The systematics of twelve species of Demospongiae from Block Island Sound and Long Island Sound is considered. Of these, two are described as new: *Haliclona loosanoffi* and *Haliclona canaliculata*. The taxonomic status of Verrill's species, *"Chalina arbuscula,"* and of de Laubenfels' species, *"Neosperiopsis deichmanni,"* is discussed.

2. Trends of variation of the skeleton of monaxonid sponges correlated with

latitude are exemplified. Megasclere size is shown to increase in northern regions in *Haliclona oculata;* styles are replaced by oxeas in the more northern of two species of *Isodictya* studied.

3. Of the twelve species considered in this work, three *(Cliona celata, Cliona lobata,* and *Cliona vastifica)* are apparently cosmopolitan in distribution. *Suberites ficus* is widely distributed in the North Pacific and North Atlantic, reaching the Mediterranean Sea and the offshore waters of northwestern Africa in the latter region. *Haliclona oculata* is found in waters of the continental shelf of Europe south to Portugal and of North America south to North Carolina.

Isodictya deichmannae and *Microciona prolifera* are both widely distributed along the North American Coast, the latter species having been reported from the Mediterranean area as well, but this requires verification. Block Island Sound is the southernmost recorded occurrence of *I. deichmannae. Halichondria bowerbanki* is found on the American Coast from the southern shores of Cape Cod to Long Island Sound and also on the coasts of England and France.

The northernmost recorded occurrence of both *Cliona truitti* and *Haliclona loosanoffi* is Long Island Sound. *Haliclona canaliculata* is known at present only from Long Island Sound.

Lissodendoryx isodictyalis is widely distributed in tropical, subtropical, and warm temperate seas. Its occurrence on the Atlantic Coast of North America as far north as Woods Hole is reported here.

II. LIFE HISTORY STUDIES

PREVIOUS WORK

Detailed studies of the life histories of sponges especially in regard to the season of larval attachment, survival after attachment, and winter survival are notably absent from the literature of this group of organisms. Such data as are recorded have usually been incidental to embryological work or to general studies of fouling organisms. Topsent (1887), however, has recorded the breeding seasons of the common sponges at Luc, on the Channel Coast of France, and Lévi (1956) has given a series of records for Roscoff, France.

The studies of Coe (1932), Coe and Allen (1937), and McDougall (1943) give some attention to the common sponges occurring in the regions of their work, and these will be summarized here.

Coe (1932) found two sponges settling on his experimental blocks at La Jolla, California. Concerning one, a simple calcareous sponge identified as a species of *Grantia* (in a later paper determined as *Rhabdodermella nuttingi* Urban), Coe observed that, whereas growth occurs throughout the winter and spring, reproduction is limited to the warmer months. An unnamed white encrusting sponge [later identified as *Leucetta losangelensis* (de L.)] is said to grow to a diameter of six inches or more from the first week in September to the following July. Presumably larvae of this species settle in late summer. In 1937 Coe and Allen reviewed the studies on the growth of sedentary marine organisms which had been carried on for nine successive years at the pier of the Scripps Institution of Oceanography at La Jolla. *Rhabdodermella nuttingi* Urban and *Leucetta losangelensis* (de L.) were described as characteristic organisms of the summer months but no precise dates of settling were indicated. It was noted that sponges are more common on blocks which have remained in the water for several months than on freshly submerged surfaces. Oyster shells were found to be especially favorable for larval sponge attachment.

McDougall (1943) made a careful study of the pile-dwelling invertebrates at Beaufort, North Carolina, and reported on two species of sponges, *Reniera tubifera* George and Wilson (=*Adocia tubifera*) and *Microciona prolifera* (Ellis and Solander). The settling period of *Adocia tubifera* was found to last only about thirty days in June and July after which the colonies spread out over the tiles, often smothering low-growing forms such as barnacles and tubicolous annelids as well as encrusting the stalks of hydroids. *Microciona prolifera* was only occasionally found on the experimental tiles although it is a common sponge in the region. Attached larvae were first noticed on August 12 and probably continued to set throughout September. Growth was most rapid and extensive on tiles just above the mud line, the finger-like processes characteristic of the species appearing on these colonies in mid-December. Although McDougall found that most species of sponges grow most vigorously during the spring months at Beaufort, he observed that *Adocia tubifera* grows best in summer and *Microciona prolifera* in winter.

McDougall discovered that current has a pronounced effect on the settling of larvae of *Adocia tubifera*. He devised a current box consisting of five chambers in each of which water flowed at a different velocity and found a predominance of settling in currents of intermediate velocity (<0.5 knot) for the Beaufort area.

No significant effect of light on the settling of *Adocia tubifera* larvae was observed by McDougall.

Pomerat and Reiner (1942) found a "small white sponge" growing on the plates which they submerged at Pensacola, Florida, in an investigation of the effects of light and surface angle on attachment of larvae. Unfortunately, they gave no information about the influence of these factors on the settling of the sponge, as well as no clue as to its identification.

A number of investigators have recorded life history notes about calcareous sponges incidental to embryological studies. Dendy (1914) found that *Grantia compressa* (Fabr.) is an annual sponge at Plymouth, England, where it grows most rapidly in the winter and spring and degenerates in autumn. The breeding season begins in early April when germ cells are abundant; mature embryos were observed leaving the oscules of sponges in June. There were also many advanced stages of embryos observed in August, although germ cells were no longer common at this time. According to Dendy, Orton has observed two breeding seasons for *Grantia compressa* at Plymouth. In June embryos are discharged from large specimens of the previous season, these colonies subsequently degenerating. The June embryos give rise to colonies which, though still very small, produce numerous embryos in October. Thus the same colonies probably breed twice during their life histories, once in late autumn and again in late spring. Jorgensen (1917, 1918) made a study of the reproductive cycle of the same species at Cullercoats, Northumberland. By examining colonies of this species every few weeks over the period of a year she was able to demonstrate that only one breeding season exists for *Grantia compressa* on the Northumberland coast. Small germ cells were first detected in June. Specimens examined in July contained both eggs and embryos; by August 17 the eggs were greatly reduced in number, but late-stage embryos were still common. No embryos were found later than early September. In these more northern waters, the colonies of the year do not seem to produce embryos in late fall as Orton observed at Plymouth.

Duboscq and Tuzet (1937) stated that all stages in the development of eggs and embryos were present in colonies of *Grantia compressa* in July at Roscoff, on the Channel Coast of France. They reported that in *Sycon raphanus* at Banyuls-sur-mer, on the other hand, the various developmental stages of germ cells and embryos tend to occur simultaneously in any one colony so that only one stage is regularly found at a time; if two stages are present, they are widely separated in age. The breeding season in this species continues from February through November.

Several authors have recorded the breeding seasons of the clionids. Grant (1826b) noted that colonies of *Cliona celata* were filled with eggs in March and April along the coasts of Scotland. Topsent (1887; 1900) has reported that specimens of this species from the Channel Coast of France are filled with eggs in the fall (late September and October). In the Mediterranean region reproduction must be earlier (probably in mid- or late summer) than in the English Channel, for Topsent (1900) found no trace of eggs in specimens from Banyuls-sur-mer during the period from October to March. Grant's observation is difficult to correlate with the more southern records which suggest that the formation of reproductive cells is initiated by high temperatures. As will be seen later, a similar correlation of breeding with temperature is also found in the western North Atlantic.

Concerning *Cliona vastifica,* Topsent (1887; 1900) has reported that eggs are abundant in the colonies in late September and October in the English Channel.

Nasonov (1883, 1924) found egg-filled colonies of *Cliona stationis* (=*C. vastifica* ?) in the Black Sea in June and July. Again the implication is that high temperatures, such as occur in mid- or late summer on the Channel coasts of France, and and earlier in the Mediterranean region, initiate the reproductive cycle.

Tuzet (1930) found eggs in *Cliona viridis* at Banyuls-sur-mer from July through September. Volz (1939) found eggs in colonies of *Cliothosa hancocki* (Topsent) at the end of April; a larva of *Thoosa mollis* Volz was observed in July. Both of these records are from Rovigno.

The observations on clionids summarized here suggest that these sponges begin their reproductive cycle when the water is warmest in temperate regions; late summer and early autumn are the seasons of egg and larva production on the coasts of northern France, in Britain, and in New England. In warm temperate regions the reproductive cycle begins earlier in the summer or even in late spring and generally lasts longer.

Topsent (1887; 1911) observed a difference in the periods of larval production in two species of *Halichondria* found along the Channel coasts of France. He found that the larvae of *H. panicea* are released in May and early June, whereas those of *H. bowerbanki* (= *coalita*) are freed in August and September.

Additional records of the breeding seasons of sponges are found in Table 24. (See also Lévi, 1956, pp. 8–9.)

METHODS

In the present study observations were made on the period of larval settling of the sponges of Milford Harbor, Connecticut, during the summers of 1947 and 1948, by suspending wire trays or bags filled with mollusc shells and rocks from a floating raft anchored in the harbor or from the dock of the Milford Biological Laboratory.

During the summer of 1947 the investigations were directed toward finding out whether boring sponges (genus *Cliona*) show any preference for particular species of molluscs and whether they settle preferentially on living molluscs or on dead shells. To this end an assortment of molluscs was planted out as listed in Table 25.

The molluscs were placed in a large wire tray (6 ft. x 3 ft. x 6 in.) which was suspended from a floating raft anchored about 50 yards from shore in water six feet deep at the mean low level. (The mean range of tides in Milford Harbor is 6.6 feet.) The tray was hanging about 3½ feet below the surface of the water so that the distance from the bottom varied from a mean of 2½ feet to a mean of nine feet, depending upon the tides. The water in which the raft was anchored was exposed to full sunlight throughout the day. The molluscs were submerged on July 7, 1947, and were examined for settled larvae at intervals thereafter.

During the summer of 1948 small wire bags (18 in. x 12 in.; see Pl. 1, fig. 6) were filled with shells and rocks and set out at weekly intervals from July 16 through September 2. Another such collector was set out on October 5. Each collector contained twelve *Crassostrea virginica* shells, two *Mercenaria mercenaria* shells, six pieces of white marble, and six pieces of phyllite, dark gray in color. The latter two materials were included to determine whether the color of the background influences settlement of larvae. The collectors were suspended from the floating dock of the Milford Biological Laboratory twenty yards from the shore at mean low tide level in a position where they were shaded from direct

TABLE 24

BREEDING SEASONS OF SPONGES*

SPECIES	BREEDING PERIOD	LOCALITY	AUTHOR
CLASS CALCAREA			
Clathrina (*Ascetta*) *clathra* (Schmidt)	Larvae released in mid-March	Bay of Naples	Schmidtlein, 1878
Clathrina (*Ascetta*) *coriacea* (Montagu)	Larvae released in October	Luc, Calvados, France	Topsent, 1887
Grantia (*Sycon*) *compressa* Fabricius	Eggs or larvae observed in August	Le Portel, France	Topsent, 1895
Leucosolenia (*Ascaltis*) *botryoides*(Ellis and Solander)	Larvae released in July	Luc, Calvados, France	Topsent, 1887
Sycandra sp.	Larvae released in August	Luc, Calvados, France	Topsent, 1887
Sycon (*Sycortis*) *ciliata* (Fabricius)	Larvae released in August	Luc, Calvados, France	Topsent, 1887
Sycon raphanus Schmidt	Larvae released from Dec. to March	Bay of Naples	Schmidtlein, 1878
Ute (*Sycon*) *glabra* Schmidt	Larvae released in early March	Bay of Naples	Schmidtlein, 1878
CLASS DEMOSPONGIAE			
Order Homosclerophora			
Oscarella (*Halisarca*) *lobularis* (Schmidt)	Larvae released in October	Luc, Calvados, France	Topsent, 1887
Oscarella lobularis (Schmidt)	Eggs or larvae observed in August	Le Portel, France	Topsent, 1895
Plakortis nigra Lévi	Eggs and sperm present in January. Hermaphroditic	Red Sea	Lévi, 1953b

(Continued)

* Names in parentheses are those used in the reference cited.

TABLE 24—Continued

BREEDING SEASONS OF SPONGES*

SPECIES	BREEDING PERIOD	LOCALITY	AUTHOR
Order Epipolasida			
Tethya aurantium (Pallas) (*T. lyncurium*)	Larvae released at end of May	Bay of Naples	Schmidtlein, 1878
Tethya aurantium (Pallas) (*T. lyncurium*)	Larvae released in September	Luc, Calvados, France	Topsent, 1887
Tethya aurantium (Pallas)	Eggs released in early August	Roscoff, France	Lévi, 1956
Order Hadromerina			
Polymastia mammillaris (Müller)	Larvae released in October	Luc, Calvados, France	Topsent, 1887
Polymastia robusta Bowerbank	Larvae released in September	Luc, Calvados, France	Topsent, 1887
Suberites (*Ficulina*) *ficus* (Johnston)	Early autumn (beginning in September)	Channel Coast of France	Topsent, 1900
Suberites ficus (Johnston)	Eggs released in early October	Roscoff, France	Lévi, 1956
Order Axinellida			
Raspailia (*Dictyocylindrus*) *ramosa* (Montagu)	Eggs observed in October	Luc, Calvados, France	Topsent, 1887
Sigmadocia (*Gellius*) *couchi* (Bowerbank)	Eggs observed in August	Le Portel, France	Topsent, 1895
Tylodesma annexa (Schmidt)	Eggs and sperm observed in September	Roscoff, France	Lévi, 1956
Vibulinus (*Dictyocylindrus*) *stuposus* (Montagu)	Eggs observed in September	Luc, Calvados, France	Topsent, 1887

(Continued)

TABLE 24—Continued

BREEDING SEASONS OF SPONGES*

SPECIES	BREEDING PERIOD	LOCALITY	AUTHOR
Order Halichondrina			
Halichondria glabra Bowerbank	Eggs or larvae observed in August	Le Portel, France	Topsent, 1895
Halichondria (*Amorphina*) sp.	Larvae released in January	Bay of Naples	Schmidtlein, 1878
Halichondria sp.	Larvae released in June	Roscoff, France	Lévi, 1956
Hymeniacidon (*Amorphina*) *caruncula* (Bowerbank)	Larvae released in September	Luc, Calvados, France	Topsent, 1887
Hymeniacidon caruncula (Bowerbank)	August and September	Channel Coast of France	Topsent, 1911
Hymeniacidon sanguinea (Grant)	Larvae released in August	Roscoff, France	Lévi, 1956
Order Poecilosclerina			
Anchinoe? (*Pronax*) *plumosa* (Montagu)	Larvae released in July, August	Isle Verte, Brittany, France	Lévi, 1956
Carmia? (*Esperia*) *lorenzi* (Schmidt)	Larvae released in October, November	Bay of Naples	Maas, 1892
Carmia? (*Desmacidon*) *similaris* (Bowerbank)	Larvae released in July	Luc, Calvados, France	Topsent, 1887
Ligrota? (*Microciona*) *spinarcus* (Carter and Hope)	Eggs or larvae observed in August	Le Portel, France	Topsent, 1895
Microciona armata Bowerbank	Larvae released in September	Luc, Calvados, France	Topsent, 1887
Mycale (*Esperia*) *lingua* (Bowerbank)	Larvae released in December	Bay of Naples	Maas, 1892
Mycale? (*Raphiodesma*) *sordida* (Bowerbank)	Larvae released in September	Luc, Calvados, France	Topsent, 1887

(Continued)

TABLE 24—Continued

BREEDING SEASONS OF SPONGES*

SPECIES	BREEDING PERIOD	LOCALITY	AUTHOR
Mycale syrinx (Schmidt)	Larvae observed in October	Bay of Naples	Wilson, 1935
Mycale (*Esperia*) sp.	Larvae released in December and January	Bay of Naples	Schmidtlein, 1878
Mycalecarmia? (*Esperella*) *littoralis* (Topsent)	Eggs or larvae observed in August	Le Portel, France	Topsent, 1895
Myxilla (*Dendoryx*) *incrustans* (Bowerbank)	Larvae released in September	Luc, Calvados, France	Topsent, 1887
Myxilla (*Dendoryx*) *incrustans* (Bowerbank)	Eggs or lavae observed in August	Le Portel, France	Topsent, 1895
Myxilla radiata Topsent	Eggs or larvae observed in August	Le Portel, France	Topsent, 1895
Plumohalichondria plumosa Arnesen	Eggs or larvae released in August	Le Portel, France	Topsent, 1895
Stylopus coriaceus (Fristedt)	Larvae released in mid-September	Isle Verte, Brittany, France	Lévi, 1956
Stylopus? (*Leptosia*) *dujardini* (Bowerbank)	Eggs or larvae released in August	Le Portel, France	Topsent, 1895
Tedanione foetida Wilson	Eggs observed in September and October	Bahamas	Wilson, 1894
Order Haplosclerina			
Acervochalina (*Chalina*) *gracilenta* (Bowerbank)	Larvae released in September	Luc, Calvados, France	Topsent, 1887
Adocia? sp.	Larvae released in December and January	Luc, Calvados, France	Topsent, 1887
Desmacidon fruticosum (Montagu)	Larvae released in April	Roscoff, France	Lévi, 1956
Gellius angulatus (Bowerbank)	Larvae released in September	Brest, France	Lévi, 1956

(Continued)

TABLE 24—Concluded

BREEDING SEASONS OF SPONGES*

SPECIES	BREEDING PERIOD	LOCALITY	AUTHOR
Haliclona indistincta (Bowerbank)	Larvae released from May to July	Isle Verte, Brittany, France	Lévi, 1956
Haliclona (*Chalina*) *oculata* (Pallas)	Larvae observed from June 15–22	Calvados, France	Topsent, 1911
Haliclona (*Chalina*) *oculata* (Pallas)	Larvae released in July	Luc, Calvados, France	Topsent, 1887
Haliclona (*Chalina*) *oculata* (Pallas)	Eggs or larvae observed in August	Le Portel, France	Topsent, 1895
Haliclona (*Reniera*) *rosea* (Bowerbank)	Larvae released in July	Luc, Calvados, France	Topsent, 1887
Haliclona (*Reniera*) *simulans* (Bowerbank)	Larvae released in August	Luc, Calvados, France	Topsent, 1887
Order Dendroceratida			
Aplysilla sulfurea Schulze	Eggs or larvae observed in August	Le Portel, France	Topsent, 1895
Halisarca dujardini Johnston	Larvae released from June to September	Luc, Calvados; Roscoff, France	Topsent, 1887; Lévi, 1956
Halisarca metschnikovi Lévi	Larvae released about June 1st	Roscoff, France	Lévi, 1956
Order Dictyoceratida			
Ircinia (*Hircinia*) *acuta* (Hyatt)	Eggs observed in September	Bahamas	Wilson, 1894
Phyllospongia foliascens (Pallas)	Larvae released in December and January	Red Sea	Lévi, 1956
Spongia officinalis Linné (*Hippospongia equina* Schmidt)	Larvae released from end of March to third week in June; most common in late May	Tunis	Vaney and Allemand-Martin, 1918

* Names in parentheses are those used in the reference cited.

TABLE 25

CULTCH PROVIDED FOR SPONGE LARVAE

SPECIES OF MOLLUSC	NO. OF LIVING SPECIMENS SET OUT	NO. OF DEAD SHELLS SET OUT
Crassostrea virginica (1 yr. old)	10 set-bearing shells	None
Crassostrea virginica (2 yrs. old)	14	4
Crassostrea virginica (3 yrs. old)	18	18
Crassostrea virginica (4 yrs. old)	14	7
Crassostrea virginica (5 yrs. old)	2	3
Crassostrea virginica (totals)	58	32
Mercenaria mercenaria	4	12
Mya arenaria	12	12
Mytilus edulis	14	None
Spisula solidissima	None	6
Arctica islandica	None	12
Pecten irradians	None	6
Ensis directus	None	8
Crepidula fornicata	None	12
TOTAL	88	100

sunlight during the greater part of the day, with the exception of a short time in the late afternoon. Examinations of the cultch were made twice monthly from August 2 through December 11.

A study was also made of the depth of maximum settling of sponge larvae in the harbor. For this work a wire cultch bag (Pl. 1, fig. 6) was suspended from the Milford Laboratory dock at each of the following depths: three feet above mean low water, at mean low water, 2½ feet below mean low water, and five feet below mean low water (bottom of harbor). Each bag was provided with 12 *Crassostrea virginica* shells and six *Mercenaria mercenaria* shells. The bags were submerged on July 14, 1947, in a location which was shaded during most of the day.

Haliclona loosanoffi was the only sponge which settled on the cultch at this site. On September 10, six shells bearing well-established colonies of this sponge were removed from the bags and were attached to tiles supported horizontally in

wooden frames so that the course of development of individual colonies could be followed. One such frame bearing three shells with a total of 22 colonies attached was suspended from the dock; another, bearing three shells with 17 attached colonies was hung from the float. A record of growth and survival in these colonies was kept, with further examinations on October 10 and December 5.

RESULTS AND DISCUSSION

Tables 26 and 27 list the total number of sponges of each species observed at each examination.

TABLE 26

SETTLING OF SPONGE LARVAE, MILFORD HARBOR, SUMMER, 1947

SPECIES OF SPONGE	DATE OF OBSERVATION						
	7/25	8/14	8/20	8/25	9/4	10/8	10/22
Halichondria bowerbanki Burton	0	0	—	3	—	—	127
Haliclona loosanoffi Hartman (on float)	0	0	—	0	—	—	29
Haliclona loosanoffi Hartman (on dock)	0	—	3	—	29	82	—
Microciona prolifera (E. and S.)	0	1	—	1	—	—	4
Cliona celata Grant	0	2	—	2	—	—	8
Cliona vastifica Hancock	0	0	—	0	—	—	1

TABLE 27

SETTLING OF SPONGE LARVAE, MILFORD HARBOR, SUMMER, 1948

SPECIES OF SPONGE	DATE OF OBSERVATION							
	August	9/2	9/23	10/5	10/19	11/2	11/18	12/1
Halichondria bowerbanki Burton	0	7	10	10	9	12	12	3
Haliclona loosanoffi Hartman	0	0	2	25	43	13	3	0

Each species is considered individually in the following discussion.

Cliona celata Grant

Larvae of this species began to settle on calcareous substrata in Milford Harbor in early August and continued to do so through early October (Table 26).

Old (1942) found eggs in the clionids of Chesapeake Bay beginning about August 1st; larvae settled on shells or calcite as early as July 28. Regrettably Old failed to record the species of clionid on which these observations were made.

Table 28 shows the distribution of the eight colonies of *Cliona celata* which settled on the cultch in the summer of 1947.

TABLE 28

SETTLING OF *CLIONA CELATA* LARVAE

SPECIES OF MOLLUSC	AGE OF MOLLUSC	NO. OF *Cliona* COLONIES
Mercenaria (alive)	3 yrs.	1
Crassostrea (alive)	3 yrs.	2
Crassostrea (alive)	4 yrs.	1
Crassostrea (alive)	5 yrs.	3
Crassostrea (shell)	2 yrs.	1

Although the number of larvae which settled is unfortunately small, an application of the chi-square test of independence to the data reveals that the association of *Cliona* larvae with oysters is significant at the 2 per cent level. In this test, infected (7 in number) and non-infected (83) oyster shells were compared with infected (1) and non-infected (97) shells of other species. The tendency for settling *Cliona* larvae to avoid oysters of the first two year classes was noted also by Topsent (1900). Doubtless the thinness of the shells of young oysters is less favorable to growth of the sponge colony within them. It is noteworthy that clionids are also rare in the thin shells of *Ensis, Mytilus,* and *Volsella.* It should also be pointed out that in the present investigations the surface area of the 24 young, living oysters was only about one-quarter of the surface area offered by the 34 larger living ones.

Of possible importance in explaining the apparent preferred settlement of *Cliona* larvae on oysters is the fact that these shells are invariably provided with corrugations and ridges which, together with the overhanging areas representing regions of active growth in previous seasons, provide sheltered locations in which the larvae can find protection from water currents during the critical periods of metamorphosis and establishment of a burrow in the shell. The question of why living molluscs attract the larvae is more difficult, though this tendency, if verified, may be associated with the water currents created by living molluscs.

On the oyster beds in the New Haven region of Long Island Sound, the incidence of infection of *Crassostrea virginica* (both living and dead) with boring sponges of the genus *Cliona* is of the order of 80 to 90 per cent. Other shells contributing to the cultch or occurring naturally on the beds and commonly bearing

the sponge are *Mercenaria mercenaria, Mya arenaria, Pecten irradians, Crepidula fornicata, Busycon canaliculatum,* and *Busycon carica.* Instances of the occurrence of *Cliona* in shells of *Ensis, Mytilus,* and *Volsella* are rare.[1]

Is the crystalline structure of the calcareous substratum of importance in excluding *Cliona* from some shells? A consideration of what is known about the method of excavation is essential to a discussion of this question. Nasonov (1883) made a very careful study of the excavating process in *Cliona stationis.* By collecting the larvae on thin calcareous plates, he was able to follow the boring process from its inception. A day or two after settling, the sponge colony had grown into a round, flat plate about 0.7 mm. in diameter, and at this time the excavating activities began. Processes of sponge tissue were sent down into the substratum dissolving the calcareous matter before them and forming initially a rosette-like pattern. At the end of the second day it was found that small hemispherical fragments of the calcareous matter were extruded from the sponge, and the colony had moved into the depression so formed. Since no spicules were present in the colony at this stage of development, Nasonov gave the first conclusive evidence against the mechanical theory of Hancock (1849, 1867). In his earlier paper this author described the existence of siliceous bodies, about 42μ across, imbedded in the surface of *Cliona* and suggested that "every portion of it will cut with the keenness of glass-paper." Later (1867) he reported that the supposed siliceous bodies were in reality fragments of conchiolin from the oyster shell being excavated. He then suggested that smaller angulated siliceous bodies (about 4μ across), also imbedded in the surface, or the spicules themselves, "must" accomplish the boring process. It is possible, of course, that both chemical processes and mechanical pressure brought about by the contractility of the sponge enter into the formation of burrows.

Old (1942) confirmed Nasonov's observations on the boring activities of recently settled clionid larvae, pointing out that many of the young sponges lack spicules when they first begin to perforate shells. He found that the sponge is able to penetrate the thin layers of conchiolin occurring between the layers of calcium carbonate in the shell. The conchiolin is removed in tiny pieces corresponding in shape to the expelled shell fragments. Although he suggests that this observation argues against the obvious hypothesis that an acid secretion is involved in the boring process, he also reports a slight daily increase in dissolved calcium in sea water containing actively boring clionids. Nasonov (1924) noted that newly settled larvae of *Cliona stationis* can perforate the periostracum of oysters in the same manner as they attack the calcareous portions of the shell. He found that the larvae also penetrate the chitin associated with the calcareous plates of *Balanus.* Nasonov suggested that the sponges probably produce an enzyme which dissolves conchiolin as well as an acid secretion which erodes calcium carbonate.

The hemispherical fragments of calcareous matter which Nasonov noted have been observed subsequently by many investigators. These fragments can be seen issuing from the oscules of *Cliona celata;* and when infected oysters are kept in a quiet aquarium for several days, piles of such fragments accumulate at the base of

[1] Nikitin (1934) reports that *Cliona stationis* is found only in the shells of *Ostrea* on the Gudaut Oyster Bank of the Black Sea coast of the Caucasus near Sukhumi. He goes on to say that "in the other regions of the Black Sea *Cliona* is met with sometimes also upon *Mytilus.*"

each oscular tube.[2] The surface of the internal cavities of an infected shell is pitted, indicating that numerous such fragments have been removed in the excavating process. These pits vary from circular to elliptical in basal cross-section, and their configuration in the shells of both *Crassostrea* and *Mercenaria* is similar to that observed by Nasonov in calcite. The shapes and dimensions of the basal cross-sections in a *Crassostrea virginica* shell were found to vary from an ellipse with axes of 45μ and 32μ to an ellipse with axes of 70μ and 58μ; circles of 45 to 50μ in diameter occurred most frequently. In a shell of *Mercenaria mercenaria* the shapes and dimensions varied from a circle 25μ in diameter to an ellipse with axes of 82μ and 50μ; circles with diameters of 45μ to 50μ again predominated. The general similarity of the boring process in the cases cited make it seem unlikely that the detailed structure of the calcareous substratum greatly influences the mechanism.

A curious observation by Cotte (1914) is suggestive of an exclusion of *Cliona* based on the composition of the substrate. He has reported a relationship between *Cliona viridis* and *Lithophyllum expansum,* in which the sponge is incapable of excavating the calcareous skeleton of the alga in order to send the characteristic tubules to the surface of the substratum. Instead, long, imperforate tubes of the coralline alga form; these are filled with sponge tissue and provided with a single apical sponge tubule through which excurrent and incurrent streams of water are maintained. The enriched supply of carbonic acid in the vicinity of the terminal oscule probably assists the alga in laying down more of the calcareous covering. It is possible that the dolomitic structure of the alga excludes *Cliona* in this case. The calcareous skeleton of coralline algae is admixed with the maximum amount of $MgCO_3$ known in any organisms [up to 36 per cent of the ash in some species (*see* Vinogradov, 1953)]. Nováček (1930) found 6.27 per cent MgO (=13.11% $MgCO_3$) in the ash of *Lithophyllum expansum*.

Vosmaer (1933) noted that large portions of colonies of *Lithophyllum* infected by *Cliona celata* are sometimes imperforate, but he also described cases in which the alga had been completely destroyed by the sponge. Volz (1939) observed nodules of coralline algae at Rovigno which were completely filled with sponge tissue and found that tubules of the sponge readily penetrate the outer covering of calcareous matter. He noted also that stages exist in which the calcareous material has been dissolved completely, leaving free-living colonies of the sponge. Similar associations of *Cliona celata* with coralline algae (*Lithothamnion* sp.) are common on the coast of central California in the experience of the present author; in no case, however, are colonies found in which tubule formation is inhibited as described by Cotte. Clionids, therefore, are certainly capable of excavating the dolomitic skeletons of corallines; the factors involved in Cotte's example remain obscure.

Topsent (1900) has noted that clionids do not infect the Portuguese oyster (*Ostrea angulata*), which has become established in places along the coast of France. It is of interest to note in this connection that Arndt (1941) failed to find any clionids on the coast of Portugal.

As the growth of *Cliona celata* colonies continues, the sponge eventually overgrows the shell and still later the shell disappears entirely, leaving a free-living

[2] This observation provides a clue as to whether the tubules of *Cliona* are functionally specialized. The restriction of such piles of calcareous fragments to the bases of tubules bearing a single terminal osculum provides evidence against the supposition sometimes held that tubules of the second type have both incurrent and excurrent functions.

sponge colony which increases in size indefinitely if undisturbed. One such colony, dredged on an oyster bed off Momauguin Beach, East Haven, Connecticut, where the bottom had been undisturbed for a period of ten years, had reached the extraordinary dimensions of 35 cm. x 16 cm. x 8 cm. Such specimens were formerly included in different genera (*Papillina suberea* Schmidt or *Raphyrus griffithsii* Parfitt).

An experiment was set up during the course of the present investigations to determine whether or not *Cliona celata* can reverse its life history. Cubes of tissue of a gamma-stage sponge (each about one cubic centimeter in volume) were attached to uninfected oyster shells. Similarly pieces of oyster shell infected with the alpha-stage of *Cliona celata* (each shell fragment having a volume of about 2 cm.^{3}) were attached to uninfected oyster shells. All were placed in a wire basket and suspended on August 22, 1947, from the dock of the Milford Laboratory at a depth midway between the bottom and mean low water (depth: 6 feet at m.l.w.). Examinations of the growth of the colonies were made at intervals thereafter. After one month of growth there was no evidence of penetration of the new shells in any case. The gamma-stage fragments had regenerated their cut surfaces and were now firmly attached to the shells on which they had been planted. Later examinations were made on October 27 and on December 17; the results at these times are shown in Tables 29 and 30.

In the gamma-stage, *Cliona celata* retains the capacity of boring into calcareous matter with which it comes into contact. It is apparent, however, that the penetration of the new substratum was accomplished more quickly by sponges of the alpha-stage than by those of the gamma-stage. This is unexpected especially in

TABLE 29

PROGRESS OF GROWTH IN THE ALPHA-STAGE TRANSPLANTS

SHELL NO.	AGE OF SHELL	SIDE OF SHELL ON WHICH SPONGE WAS PLANTED	PENETRATION INTO NEW SHELL*	
			October 27	December 17
1	2 yrs.	Lower	12–upper surface	20–upper surface
2	2 yrs.	Upper	1–lower surface	3–lower surface
3	3 yrs.	Lower	9–upper surface	12–upper surface
4	3 yrs.	Upper	13–lower surface	24–lower surface
5	4 yrs.	Lower	7–upper surface	22–upper surface
6	4 yrs.	Upper	Sponge fragment lost	—
7	5 yrs.	Lower	18–upper surface	18–upper surface
8	6 yrs.	Upper	None-lower surface	3–lower surface

* In terms of number of holes in surface of shell on side opposite that on which sponge was planted.

TABLE 30

PROGRESS OF GROWTH IN THE GAMMA-STAGE TRANSPLANTS

SHELL NO.	AGE OF SHELL	SIDE OF SHELL ON WHICH SPONGE WAS PLANTED	PENETRATION INTO NEW SHELL*	
			October 27	December 17
1	2 yrs.	Upper	Sponge fragment lost	—
2	3 yrs.	Lower	Sponge fragment lost	—
3	3 yrs.	Upper	No evidence of penetration	3–lower surface
4	4 yrs.	Lower	No evidence of penetration	6–upper surface
5	4 yrs.	Lower	No evidence of penetration	None–upper surface Many–under sponge, lower surface
6	5 yrs.	Upper	No evidence of penetration	4–lower surface
7	5 yrs.	Lower	No evidence of penetration	None–upper surface Many–under sponge, lower surface
8	6 yrs.	Upper	2–under sponge, upper surface	6–lower surface

* In terms of number of holes in surface of shell on side opposite that on which sponge was planted.

view of the fact that more sponge surface is in contact with the shell in the case of the gamma-stage transplants, and one would suppose that immediate penetration of the shell would ensue. Instead, as Table 30 indicates, there were no cases of excavation through the entire thickness of the shell by the gamma-stage fragments even two months after affixation, whereas in every case but one, the alpha-stage fragments had accomplished a complete penetration of the shell so that from one to 18 holes were present on the side of the shell opposite that on which the transplant had been attached. On December 17, four of the six gamma-stage transplants had bored completely through the shells with a mean of five holes (range, three–six) whereas all seven of the alpha-stage transplants had penetrated completely with a mean of 15 holes (range, three–24). Why there should be a longer latent period in the case of the gamma-stage colonies is difficult to say; perhaps the delay simply reflects a period necessary for the regeneration of the cut surfaces of the free-living samples.

Although the gamma-stage will grow either as a free-living colony or revert to the boring habit, it has, to the writer's knowledge, never been demonstrated that larvae can grow directly into the gamma-stage without passing through a boring or

alpha-stage. Seemingly in the early stages of growth, the colony requires the protection provided by mollusc shells and other calcareous matter into which it bores. It would be instructive to attempt to rear larvae under laboratory conditions in the absence of calcareous substrata to find out whether attachment takes place on other substances and how far development proceeds under these conditions. On the other hand, small portions of colonies already established in oyster shells might be isolated from their calcareous substratum to find out if survival in the free-living stage is dependent upon size or age of colony. During the summer of 1949, small cubes (one cm.^{3}) of gamma-stage tissue were planted on phyllite slabs; their growth was followed for three months after transplantation. Growth was slow and consisted mainly of a spreading out over the rock from the base of the fragment.

In Vosmaer's exhaustive account of the genus *Spirastrella* (1911) he mentions certain forms of the highly variable species,[3] *S. purpurea,* which dwell in cavities in calcareous matter. There is no evidence in these instances that the sponge colonies have excavated the cavities; they simply inhabit abandoned worm tubes and other similar situations. These forms are so characteristically associated with cavities that many authors have mistaken them for true boring sponges. Other forms of what Vosmaer regarded as the same species live on the surface of corals and shells, lacking the tendency to dwell in cavities. This observation provides a clue to the origin of the boring habit. It is not unlikely that a cavity-dwelling tendency resulted in the establishment of a process by which the cavities could be enlarged. After this process had appeared, the sponge was capable of establishing its own cavities and was no longer restricted by fortuitous settling in naturally occurring ones.

Cliona vastifica Hancock

Only a single colony of *Cliona vastifica* settled on the shells set out. It occurred in the shell of a five-year oyster and had probably settled some time during the month of September, the first date of observation having been October 13, 1947, at which time the colony was well established. Topsent (1900) found individuals of this species filled with orange unicellular eggs in late September in the English Channel. Reproduction would therefore seem to be somewhat later there. In the New Haven Harbor region of Long Island Sound this species is never as abundant as *Cliona celata,* a fact borne out in the Milford Harbor larval settling observations.

Cliona vastifica has never been observed to overgrow its shell and assume a free-living condition. This is surprising since a point must be reached in the development of the sponge colony when the shell in which it is growing is completely occupied by sponge tissue, so that further growth can result in but one thing: overgrowth of the shell. It is impossible to say at present whether this observed difference between the two species, *Cliona celata* and *C. vastifica,* is a result of a slower rate of growth or perhaps a shorter life span in the latter form.

An interesting mode of asexual reproduction was observed in specimens of *Cliona vastifica* which had been kept in aquaria in the Milford Laboratory for several weeks during the summer of 1947. Protruding from certain of the holes in the shell harboring the sponge were long, thin tubes bearing bulbous expansions along their length. It is uncertain whether these tubules possessed any incurrent

[3] In a later monograph, Vosmaer (1933, p. 334) was inclined to regard *Cliona* and *Spirastrella* as synonyms.

or excurrent function, but it seems most likely that the rounded bodies were occasionally freed from their attachment and thus served to establish new colonies in other shells. Indeed, it is possible that these structures are provided with cilia at the time of their release much as the asexually produced larvae described by Wilson (1894). This method of reproduction was observed by Merejkowsky (1879) in *Rinalda arctica* (=*Polymastia mammillaris*) occurring in the White Sea and was subsequently observed by Arnesen (1917) in the same species. It is probably not an uncommon method of reproduction in tubule-bearing species of Hadromerina, but it has been very generally overlooked.

Perhaps the most interesting problem presented by *Cliona vastifica* is its occurrence along with the commoner *Cliona celata* and the rarer *Cliona lobata* in what seems to be a competitive relationship. A further consideration of this matter will be deferred until the results of salinity tolerance experiments in the several species have been discussed.

Haliclona loosanoffi Hartman

This sponge is one of the most common species found in Milford Harbor, and comparatively large numbers of settled larvae were observed during both seasons of study, providing an opportunity to obtain information on the period of larval settling as well as the survival of the young colonies. In 1947 data regarding this species were secured from two sources: (1) the molluscs in the tray suspended from the float in Milford Harbor, (2) the cultch bags set out at varying depths from the dock.

Haliclona loosanoffi larvae began settling in mid-August in 1947 and in mid-September in 1948. In both years the peak of settling had been reached by early October as is shown in figure 28.

The growth of 39 colonies of *Haliclona loosanoffi* was followed in greater detail from September 10, 1947 to December 5, 1947. These observations are listed in Table 32 and summarized in Table 31.

An attempt has been made to construct a life table for *Haliclona loosanoffi* although the data are meager. It must be emphasized, however, that this analysis pertains to only one part of the life cycle, extending from the time of establish-

TABLE 31

SURVIVAL OF *HALICLONA LOOSANOFFI*

LOCATION OF SPONGES	NO. OF COLONIES Sept. 10	NO. OF COLONIES Oct. 10	NO. OF COLONIES WHICH SETTLED SINCE Sept. 10	NO. OF COLONIES WITH GEMMULES Oct. 10	NO. OF COLONIES WITH GEMMULES Dec. 5	NO. OF GEMMULES Dec. 5
Sponges on dock	21	9	1	1	6	440
Sponges on float	18	10	1	1	6	105
TOTAL	39	19	2	2	12	545

ment of the young sessile colonies which have recently metamorphosed from free-swimming larvae up to the time of gemmule formation and winter killing. A source of error results from the fact that the exact date of settling is unknown for the 39 colonies studied. It can be stated only that they settled some time beween August 20 and September 10, a three-week period which may represent the spread in their ages. Survival was recorded on September 10, October 10, and December 5. On November 10 it was observed that all colonies had died back, but no detailed record of gemmulation was kept. Presumably the observations on that date would have been identical with those on December 5, although fragmentation of the gemmules following death of the colony is not impossible.

TABLE 32

DATA ON GROWTH OF SELECTED COLONIES OF *HALICLONA LOOSANOFFI*

SHELL NO.	COLONY NO.	VOLUME INDEX† Sept. 10	VOLUME INDEX Oct. 10	RATIO OF VOLUMES	NO. OF GEMMULES Dec. 5
I-A.....	1	570	3850** (831)*	6.8 (1.5)*	350
	2	—	84	—	—
I-B.....	1	319	—	—	—
	2	158	—	—	—
	3	94	—	—	—
	4	27	108	4.0	20
	5	27	—	—	—
	6	27	—	—	—
	7	87	—	—	—
	8	27	—	—	—
	9	27	—	—	—
	10	27	—	—	—
	11	54	—	—	—
	12	27	—	—	—
	13	32	173	5.4	—
I-C.....	1	248	450** (241)*	1.8 (1.0)*	—
	2	8	—	—	—
	3	98	54	0.5	11
	4	180	—	—	—
	5	275	206	0.8	37
	6	106	958	9.0	14
	7	196	178	0.9	8
II-A.....	1	36	—	—	—
	2	4	—	—	—
	3	51	140	2.7	20
	4	198	248**	1.3	—
	5	36	32	0.9	—

(Continued)

TABLE 32—Concluded

SHELL NO.	COLONY NO.	VOLUME INDEX† Sept. 10	VOLUME INDEX Oct. 10	RATIO OF VOLUMES	NO. OF GEMMULES Dec. 5
II-A (Cont.)	6	105	—	—	—
	7	27	60	2.2	9
	8	24	—	—	—
	9	18	42	2.3	—
	10	93	—	—	—
	11	—	48	—	7
II-B.....	1	3	—	—	—
	2	75	—	—	—
	3	150	27	0.2	23
	4	193	3875	20.0	—
	5	88	—	—	—
II-C.....	1	342	288	0.8	—
	2	27	421	15.6	32
	3	24	25	1.1	14

* Living tissue. Rest of colony dead.
** Gemules present on Oct. 10.
† Volume index = product of length × width × height. Mean ratio of volumes — 4.2
I—Shells so marked were suspended from dock.
II—Shells so marked were suspended from float.

In spite of the weaknesses of the data a life table is presented (Table 33) in order that survival may be compared with data existent for other sessile marine organisms (Deevey, 1947).

TABLE 33

LIFE TABLE FOR NEWLY SETTLED COLONIES OF *HALICLONA LOOSANOFFI*

x AGE IN MONTHS	d_x NO. DYING IN INTERVAL OUT OF 1000 SETTLED LARVAE	1_x NO. SURVIVING AT BEGINNING OF AGE INTERVAL OUT OF 1000 SETTLED LARVAE	$1000\ q_x$ MORTALITY RATE PER 1000 ALIVE AT BEGINNING OF AGE INTERVAL
0–1	564	1000	564
1–2	154	436	353
2–3	0	282	0

Data on the number of free-swimming larvae which are produced and the percentage of these which settle successfully will be necessary to complete the picture, but such are unavailable at present. As it stands, the survivorship curve approaches that of Pearl and Miner's (1935) positively skew rectangular type in which there is heavy mortality in early life with long survival of the few individuals which live to advanced ages.

Probable causes of death of newly settled sponges are several and are dependent in part upon time. Predation by gastropods is very probably an important cause of mortality. Nudibranchs have long been suspected of browsing on sponge tissue, and recently Burton (1949) has demonstrated that snails and limpets do not pass by this spiculous fare. He observed spicules in the guts of *Littorina littorea* and *L. obtusata* as well as *Patella,* and found grazed areas on the sponge colonies from which the molluscs were removed. The present writer has observed that chitons likewise feed on sponges on the central California coast. Crowding by faster growing organisms may be of some importance, but on the whole, sponges are able to hold their own by encrusting such organisms as tunicates, bryozoans, and barnacles. In certain cases coalescence of several colonies may occur and introduce an error. And in other instances parts of a large colony will degenerate leaving several isolated portions to continue; these cases are easily detected, however, by the continuity of the skeletal framework. Some of the sponges which survive until late October without having produced gemmules, will succumb to decreasing temperature conditions, a problem discussed at greater length in a later section.

Data on the winter survival of gemmules are also unavailable. The gemmules reported here were kept in a tray in Milford Harbor during the winter of 1947-48 in anticipation of securing information on their survival. However, when the shells to which they had been attached were examined in the spring, no trace of the gemmules could be found. Presumably they had all sloughed off during the rigorous winter of that year. Provided that the gemmules remain attached to their original substratum during the entire winter, it is likely that the same number of colonies would start growth in the spring as had formed gemmules in the fall. The germination of but one gemmule would suffice to renew the growth of the colony, and the germination of many gemmules (from the same fall colony) would lead to a single, large colony since the young sponges produced from the individual gemmules would doubtless coalesce. In such a case, the survivorship curve could be continued as a straight line up to the time of early growth of the sponge colonies the following year.

If, on the other hand, the gemmules regularly slough off, as was the case with those under observation in Milford Harbor, then renewed growth in the spring must depend upon the number of gemmules which come to rest on a suitable substratum at the time of germination. A great increase in the number of colonies could result from this series of events, as is shown by the 1947 data where 12 colonies produced 545 gemmules. Another uncertainty which arises in regard to the role played by gemmules in increasing the population in this species, concerns the type of organism produced upon germination. Observations of gemmules which germinated during the winter in the laboratory revealed that sessile colonies arise directly from the gemmules in this case; however, it has been shown by Wilson (1894) that the gemmules of some monaxonid sponges give rise to ciliated larvae essentially like those produced sexually. If this is an alternative mode of germination in *Haliclona loosanoffi,* the gemmules are unquestionably important

agents of population increase. A solution to these problems awaits more careful and complete observations on the life history of this interesting sponge.

Reference to the graph in figure 28 indicates that the larvae settling on shells suspended from the dock considerably outnumbered those settling on shells hung from the float. Since the shells in the latter location outnumbered the former, so that there was actually more surface area available for settling, it seems reasonable to expect a correlation with some environmental factor. The only obvious differ-

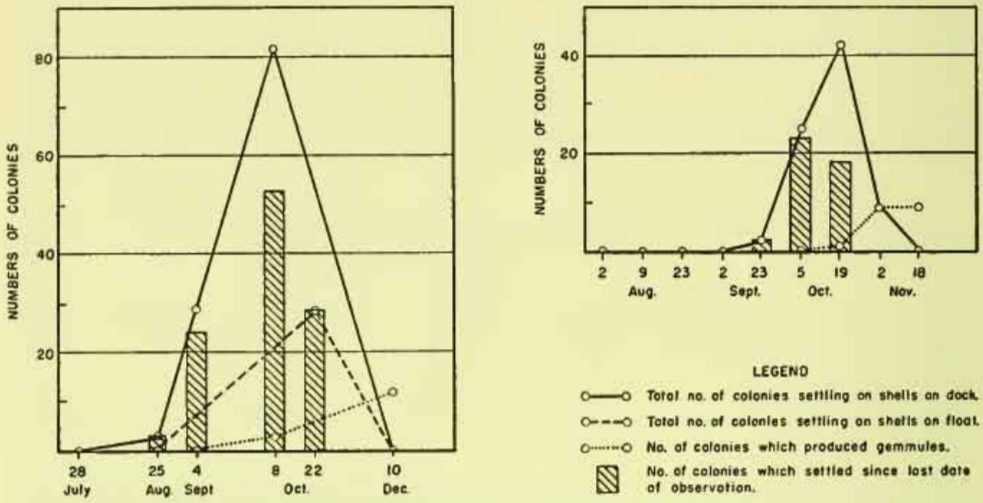


FIGURE 28. Larval settling of *Haliclona loosanoffi* in two successive years. Milford Harbor. Left, 1947; right, 1948.

ence in the two locations concerns the amount of sunlight which reached them. The float received the full light of the sun all day whereas the shell bags, suspended from the dock, were shaded. In the other localities in Long Island Sound where this species has been taken, the colonies are invariably located on the undersides of overhanging granite blocks or on the lower sides of intertidal rocks and boulders. They have never been taken in exposed situations as is true of *Halichondria bowerbanki*. The numbers of colonies of the two species, *Haliclona loosanoffi* and *Halichondria bowerbanki*, which settled in exposed and shaded situations in the two successive years are shown in Table 34.

TABLE 34
INFLUENCE OF LIGHT ON SETTLING OF SPONGE LARVAE

SPECIES OF SPONGE	LARVAE SETTLING IN FULL SUN 1947	LARVAE SETTLING IN SHADE 1947	LARVAE SETTLING IN SHADE 1948
Halichondria bowerbanki (Max. no. settling)	64	0	12
Haliclona loosanoffi (Max. no. settling)	29	82	43

On the other hand, an anlysis of settling on white marble as opposed to dark gray phyllite fails to show any tendency for one to be favored over the other. Comparison of settling on both of these substrata, as well as on shells of *Crassostrea virginica* (fig. 29) reveals that settling on the several types of backgrounds was essentially random. In the figure, half the total number of colonies which settled on oyster shells is shaded so as to permit comparison with similar surface areas on marble and phyllite.

It is of interest to note that McDougall (1943) found that *Adocia tubifera* was the only organism which settled in his light box at random. McDougall pointed

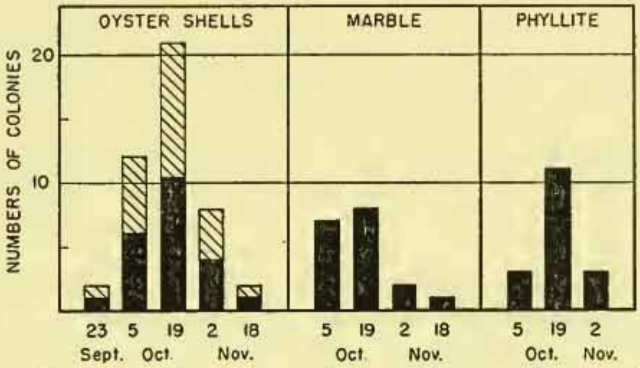


FIGURE 29. Larval settling of *Haliclona loosanoffi* in relation to color of substratum. See text.

out that the glass top on his box eliminated ultra-violet radiation which may be the injurious element of sunlight for some organisms. However, the amount of ultra-violet light which penetrates turbid coastal waters is probably insignificantly low, at least at a depth of 1½ meters at which these organisms settled. Consequently, it is likely that a basic difference in phototactic responses exists in these two species.

The distribution of *Haliclona loosanoffi* colonies with depth is shown in Table 35. Their exclusion from the shells on the bottom is doubtless a result of the heavy silting in the Harbor so that only those colonies could survive which settled on substrata suspended off the bottom where water currents were more likely to be effective in preventing silt accumulation. The upper limit of settling found here agrees with field observations elsewhere in the Sound where, in general, mean low water represents the shoreward extreme of distribution.

Haliclona loosanoffi colonies were observed to die back in mid-November each year from 1947 through 1949. The regularity with which the colonies perished each fall suggests that an environmental factor is limiting their growth. The degenerative process actually begins in late October or early November when the living tissue of portions of the colonies dies back leaving the bare skeletal framework. This degeneration proceeds slowly through the next few weeks until all sponges have died by the end of the second week of November. In figure 30, the surface water temperatures taken at high tide in Milford Harbor during the months of October and November for the past three years are plotted along with observations on the survival of colonies of *Haliclona loosanoffi*. In 1947 *Haliclona* colonies were observed to be growing normally on October 10 and 22, but by

TABLE 35

LARVAL SETTLING OF *HALICLONA LOOSANOFFI* IN RELATION TO DEPTH

DEPTH	NUMBER OF COLONIES		
	August 27, 1947	September 4, 1947	October 8, 1947
3 feet above mean low water	—	—	—
Mean low water level	—	4	37
2.5 feet below mean low water	3	24	45
5 feet below mean low water	—	1	—

November 10, all had died back leaving the skeleton and gemmules. During this period the water temperatures had fallen from 17° C. to 11.6° C. In the following year the colonies were thriving on October 5; by October 19 one colony had begun to die back. On November 2 only four (out of 42) colonies were still in a

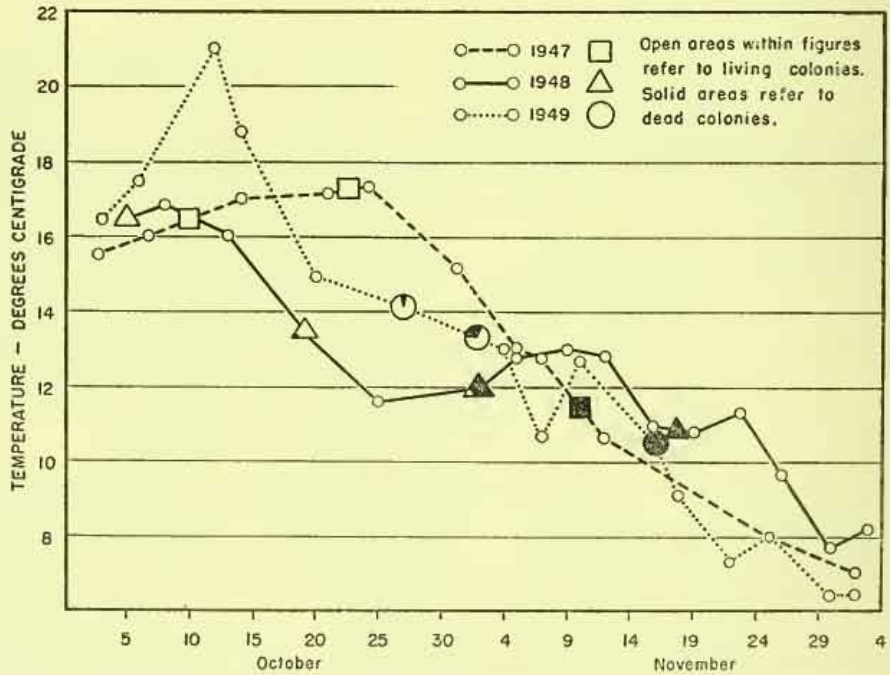


FIGURE 30. Graph comparing Milford Harbor water temperatures (surface, high tide) with onset of degeneration in colonies of *Haliclona loosanoffi* over a three-year period.

healthy condition; five others were partially alive. All the rest had died back completely with only four of these leaving gemmules to carry them over the winter. On November 18 all colonies were dead; nine had formed gemmules. In 1949 a few colonies showed indications of degeneration on October 27; this process was more extensive by November 2; all colonies were dead on November 16.

It is apparent from the graph that each year as the temperature fell below 16° C., degeneration began. It is impossible to set the limiting temperature very exactly without experimental data; but the critical range certainly lies between 16° and 12° C.

Since this sponge is able to survive the winter in the gemmule state, winter killing in itself is probably not a factor in limiting northward distribution. The minimum temperature for reproduction would seem to be of greater importance in this regard. The first date on which newly settled colonies of this sponge were recorded during the three summers of observation is distinctly correlated with the water temperatures of the season in question as can be seen in figure 31. Precise information about the timing of the early processes of the reproductive cycle are unfortunately not available; nor are there any experimental data on the effect of temperature on the reproductive cycle. It is therefore futile to postulate exact

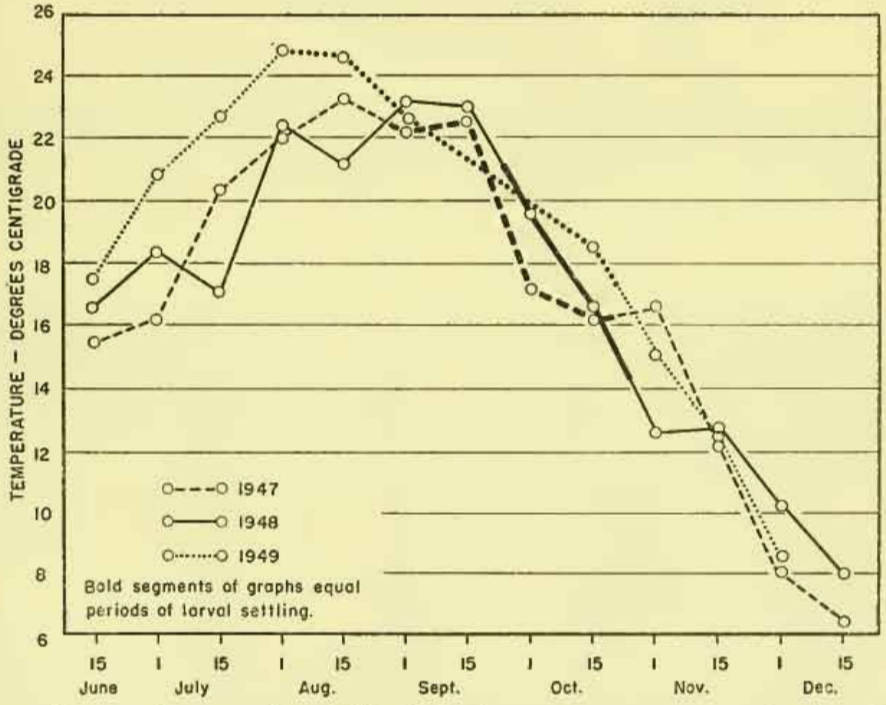


FIGURE 31. Graph comparing Milford Harbor water temperatures (surface, high tide) with onset of larval settling in *Haliclona loosanoffi* over a three-year period.

limiting temperatures in this discussion. However, the data at hand imply that there is a certain minimum temperature (probably between 20-22° C.) at which the reproductive process begins, and that the annual variation in appearance of this temperature is reflected in the observations on larval settling.

Perhaps the length of growing season which remains after the larvae have settled and metamorphosed is of equal importance in limiting the northward distribution of this sponge as the minimum temperature for repopulation. The former time interval is, of course, dependent upon the latter; its importance concerns the number of gemmules which are available for repopulation in the spring. Table 36 indicates that the number of sponges which formed gemmules in 1947 was greater than that in 1948, and although these data are found to be insignificant when the chi-square test is applied, the number of gemmules formed per sponge in 1947 was distinctly higher than that in 1948.

TABLE 36

GEMMULE FORMATION IN SUCCESSIVE YEARS

YEAR OF OBSERVATION	NO. OF COLONIES OBSERVED	NO. OF COLONIES WITH GEMMULES
1947	39	12
1948	42	9

Exact counts of the gemmules produced in 1948 were not made, but the number was surely no higher than one-fourth of the 545 gemmules produced by 12 colonies in 1947. It seems likely that this difference resulted from the longer growth period in 1947 with the consequent larger size of the colonies.

Halichondria bowerbanki Burton

Young *Halichondria bowerbanki* colonies were first observed during the last week of August in 1947 and in early September in 1948. Settling continues from that time through October and in 1948, at least, it extended into late November or possibly early December, three colonies having settled between November 18 and December 11 (see fig. 33). Subsequent survival of the colonies proved to depend upon the severity of the winter. During the rigorous winter of 1947–48, all colonies were killed back in Milford Harbor. On the other hand, during the mild weather of the 1948–49 winter season, the colonies which had settled in the fall of 1948 survived and continued growth slowly. Some of these colonies were still growing in the Harbor in mid-December of 1949, though all had noticeably declined in vigor toward the end of their second fall season.

Essentially similar observations in regard to the importance of winter-killing in determining the abundance of *Halichondria bowerbanki* in inshore locations, were made at Momauguin (East Haven) and Pine Orchard (Branford), Connecticut. In the former locality, large colonies of *Halichondria bowerbanki* were abundant during the summer of 1947 on the reefs surrounding Stony Island offshore from Momauguin Beach. During the following summer, however, such large colonies of this sponge were nowhere to be seen in this vicinity. There were numerous small colonies encrusting the algae and rocks in the vicinity suggesting that the area had been recolonized by asexually or sexually produced larvae from colonies which had survived the severe winter of 1947–48 in deeper, offshore waters. During

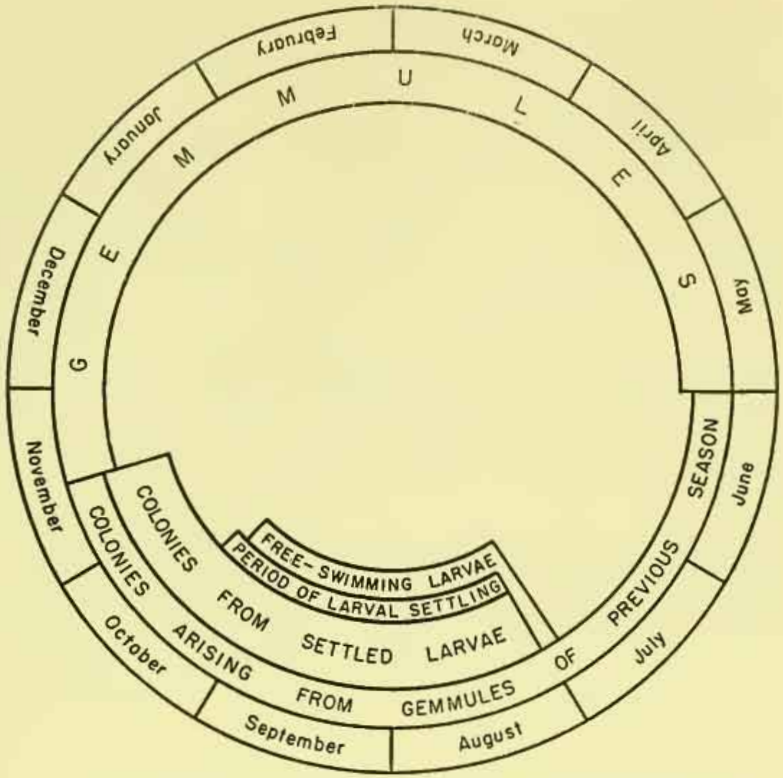


FIGURE 32. Chart summarizing the life history of *Haliclona loosanoffi*.

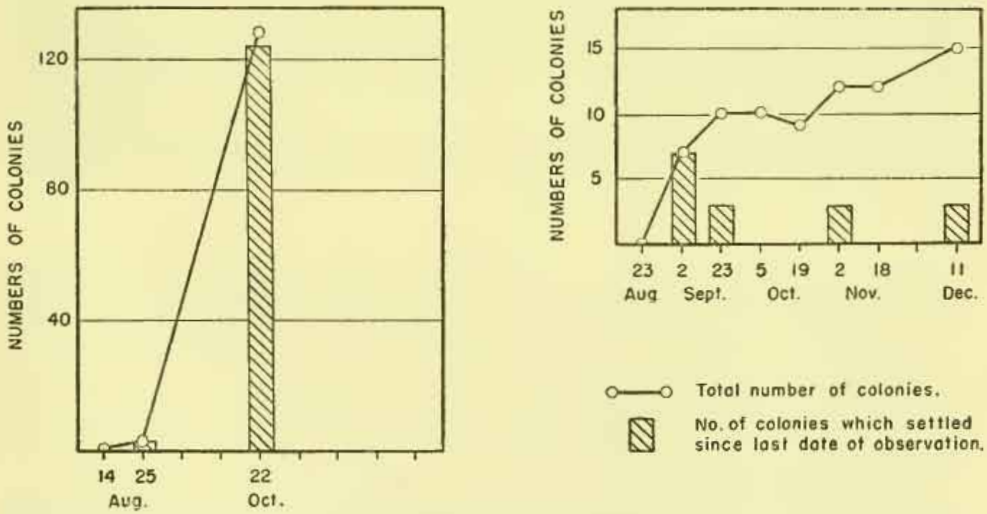


FIGURE 33. Larval settling of *Halichondria bowerbanki* in two successive years. Milford Harbor. Left, 1947; right, 1948.

the summer of 1949, conditions similar to those in 1947 prevailed with large sized colonies abundantly in evidence. These colonies had doubtless lived throughout the mild winter of 1948–49 and were ready to start rapid growth with the onset of warm weather in the spring.

In the fall of 1948 a large number of young colonies of *Halichondria bowerbanki* were observed growing between extreme low water neaps and extreme low water springs on Tub Island, off Pine Orchard, Connecticut. These young sponges measured from two to five centimeters in diameter and were growing at a density of about three per square meter on the northern end of the island, frequently in exposed places on the bare granite surface. The following spring, virtually all these colonies had disappeared except for the few which had settled in crevices, under overhanging rocks, or in other protected spots. Winter killing and predation by snails probably account for the mortality of the greater number of these colonies, but it is noteworthy that some of the colonies were able to survive through the mild winter of 1948–49.

A discussion of the relation of light to settling in this species has already been undertaken.

In regard to the intertidal distribution of this sponge, it is of regular occurrence in tidal pools and on the surfaces of rocks at Lighthouse Point (New Haven), Double Beach (Branford), Pine Orchard (Branford), Stony Creek, and Hammonasset, Connecticut. It seldom survives higher than the level of extreme low tide neaps, but in one instance, a thriving colony was observed in a tide pool at Double Beach located just above the mid-tide level. With this one exception, these observations on the intertidal distribution of *Halichondria bowerbanki* agree with those of Burton (1949) on *H. panicea* at Tor Bay, England.

Microciona prolifera (Ellis and Solander)

Microciona prolifera is an abundant sponge on the oyster beds of Long Island Sound; it is surprising that so few were observed in the present investigations. Reference to Table 26 indicates that it began settling in early August and continued up to mid-October. McDougall (1943) found essentially the same settling period for this species in Beaufort Harbor, North Carolina. It is possible that this species, like *Halichondria bowerbanki,* prefers well-lighted situations, for it was not found on any of the cultch set out from the dock in a shaded location. It is certainly true that intertidal and shallow water specimens of this sponge commonly grow in exposed situations and are not restricted to the undersides of rocks as is true of *Haliclona loosanoffi.*

SUMMARY

1. In this investigation *Cliona celata* larvae showed a significant tendency to settle preferentially on shells of oysters. It is suggested that the many irregularities of the surfaces of these shells favor settlement of clionid larvae.
2. The massive gamma-stage of *Cliona celata* is capable of reverting to the boring habit when cuttings are applied to a calcareous substratum.
3. The formation of strands of spherical buds was observed as a mode of asexual reproduction in *Cliona vastifica.*
4. A life table constructed from a limited amount of data on the survival and death rates of newly settled *Haliclona loosanoffi* colonies shows that it is of the positively skew rectangular type and is allied to that of other sessile marine organisms such as barnacles.

5. Larvae of *Haliclona loosanoffi* tend to respond negatively to light, contrary to the larvae of *Adocia tubifera,* observed by McDougall at Beaufort, North Carolina, which are unaffected by light in choosing a place to settle.
6. The relationship of depth to larval settling was studied in *Haliclona loosanoffi.* Heaviest settling occurred on shells at mean low tide level and on those suspended freely in the water at 2½ feet below mean low water. No settling occurred at the bottom.
7. Data accumulated over a period of three years reveal that in *Haliclona loosanoffi,* the time of settling of larvae fluctuates annually in relation to temperature; larvae are released shortly after the highest water temperatures of the year.
8. Degeneration of newly settled colonies of *Haliclona loosanoffi* also fluctuates annually in relation to water temperature. In general, temperatures of 16° C. or 15° C. lead to the inception of degeneration.
9. It is suggested that two factors operate in limiting the northern distribution of this sponge: (a) the minimum temperature at which reproduction can occur; (b) the length of growing season which remains after the larvae have settled, a factor which will determine the number of gemmules produced.
10. *Halichondria bowerbanki,* which has no winter-resistant gemmules, survives the winter in inshore waters in abundance only during mild years. After severe winters, recolonization on the inshore areas is largely dependent upon larvae from colonies in deeper offshore waters.

III. SALINITY TOLERANCE, COMPETITION FOR SUBSTRATE, AND DISTRIBUTION AMONG CLIONIDS

INTRODUCTION

Although Long Island Sound opens into the Atlantic Ocean at both ends, its western outlet is very narrow, preventing a rapid interchange of water between the open ocean and the Sound, and the salinity is somewhat reduced. Galtsoff and Loosanoff (1939) found that during August and September the bottom salinity of the Sound varies gradually from 32 o/oo at its eastern end to 26 o/oo near New York City. They reported that seasonal variations are small, the range in any one locality seldom exceeding 1 to 2 o/oo during the year's cycle. The difference in the salinity of water in the middle of the Sound from that of adjacent inshore localities is also slight, seldom more than 1 o/oo. According to a recent survey made by Riley (1956), the annual range of salinities at stations in the central part of the Sound is 4 to 5 o/oo.

The fauna of the greater part of Long Island Sound thus falls into the polyhaline zone (16.5 o/oo to 30 o/oo) proposed in the scheme of classification of brackish waters of Redeke (1922) as modified by Välikangas (1933). Remane (1934) has doubted the validity of a polyhaline zone, pointing out that in waters with salinities ranging down to 16.5 o/oo, there is simply a decrease in the numbers of marine species with few or no distinct brackish water species to be found. Dahl (1948) has criticized Remane's conclusions because of the latter's use of mean salinity values in a region (Kiel Bay) where great variations in salinity occur. Dahl has given ample evidence of the existence of distinctive animal communities living on algae in the polyhaline zone. Few, if any, of the species are confined to this zone, but many have the center of their ranges here. He has emphasized that in defining the lower limits of the marine zone, not only the the mean value, but also the stability of the salinity factor is of importance. On the basis of his studies of arthropods living on marine algae in the Skagerrak and northern Cattegat, he was able to establish the lower limit of the marine zone there at 27–28 o/oo, provided the variation coefficient is lower than 15. At one station in the southern Cattegat, a mean salinity of 28 o/oo is combined with a variation coefficient of 20, a range probably below that which a marine fauna can endure. For a less stable area such as this, a value of 30–31 o/oo is a more likely lower limit. Judging from the stable bottom salinity conditions found by Galtsoff and Loosanoff and by Riley in Long Island Sound, this locality would be an excellent one in which to study the polyhaline zone and its boundary with the marine zone.

In the present study an attempt was made to determine the influence of salinity tolerance on the distribution of five species of Long Island Sound sponges. Work on three of these was soon abandoned because of difficulties in determining death points. A satisfactory survival index was worked out for *Cliona celata* and *C. vastifica*, however, and the results of salinity tolerance experiments on these are reported, together with some observations on the distribution of these two species and the possible importance of competition for substrate as a factor in speciation.

Previous experimental work on the salinity tolerances of sponges has been limited to determining the effects of diluted sea water on reunition bodies. Galtsoff (1925) found that dissociated cells of *Microciona prolifera* (Ellis and Solander) failed to coalesce in hypotonic sea water with concentrations lower than 12.4 to 9.3 o/oo. He found that the cells are more sensitive to an increase in osmotic pressure than to a decrease, coalescence taking place in hypertonic solutions up to a value of 55.8 o/oo. De Laubenfels (1932a) found that dissociated cells of *Iotrochota birotulata* Higgin coalesced normally in solutions ranging from 80 per cent sea water (28 o/oo) to 110 per cent sea water (38.5 o/oo). Above and below these values, the number of cell aggregates per unit area was lower.

SALINITY TOLERANCES

Methods: Experiments to determine the salinity tolerances of *Cliona celata* and *Cliona vastifica* were undertaken at the Biological Laboratory, U. S. Fish and Wildlife Service, Milford, Connecticut, concurrently with similar experiments on oysters being conducted by Dr. V. L. Loosanoff and his staff. Colonies of the alpha-stage of *Cliona celata* and colonies of *Cliona vastifica,* both inhabiting the shells of living *Crassostrea virginica,* were exposed for varying lengths of time to salinities ranging from 27 o/oo to fresh water. The infected oysters used were of approximately the same size and harbored colonies of sponges of similar sizes. The oysters were collected on state leased oyster beds off Charles Island, Milford, and in New Haven Harbor, at stations of essentially similar depth and salinity characteristics.

The initial set of experiments was run by placing the oysters infected with sponge colonies in photographic trays supplied with running water of the following six concentrations: (1) 26–27 o/oo (Milford Harbor water, collected at high tide), (2) 20 o/oo, (3) 15 o/oo, (4) 10 o/oo, (5) 5 o/oo, (6) fresh tap water.

The diluted concentrations were prepared in the following manner: A 5-liter reservoir jar was kept filled with sea water up to the level of an overflow spout. A similar jar was kept filled with fresh tap water. In this way a constant level was maintained in each jar so that an equal pressure was applied at all times to the outlet tubes leading from the bottom of each jar. To obtain a given diluted concentration, an outlet tube from each reservoir jar was led into a beaker in which the water had a chance to mix thoroughly before overflowing into the culture tray. A constant supply of a culture of *"Chlorella"* and miscellaneous flagellates was introduced, dropwise, into the sea water reservoir.

The concentrations of water in the trays varied no more than 0.5 o/oo on either side of the desired value. Hydrometric salinity determinations were made twice daily to check this value.

After the initial experiments had demonstrated an approximate range for survival, a set of less widely spaced concentrations was tried in the critical range, including the following two series: (1) 12 o/oo, 9 o/oo, 7.5 or 6 o/oo, 3 o/oo, (2) 13 o/oo, 10 o/oo, 5 o/oo, 3 o/oo.

The experimental animals were exposed to the various concentrations of sea water for periods of time ranging from one hour to one week and were in each case transferred to sea water after exposure in order to note recovery. Observations were made during the course of and at the end of the period of exposure to experimental conditions and also after a period of recovery in Milford Harbor water (salinity, 26–27 o/oo).

Results: Under normal conditions *Cliona celata* bears ostia or incurrent pores

(from 5–10 in number) on the flattened summits of tubules which protrude from holes in the surface of the calcareous substratum (Pl. 1, fig. 2). Oscules are borne individually on lower, wider tubules. *Cliona vastifica,* on the other hand, bears both a single osculum and a group of ostia on every tubule.[1] These structures are illustrated by Volz (1939). The tubules in both species are capable of contraction into the inner recesses of the calcareous substratum so that the sponge tissue is level with the surface of the substratum, and water currents through the sponge cease. This fact provides the most readily observable criterion for cessation of activity in these organisms. Intermediate stages occur in which the tubules are partially contracted and in which there is doubtless a reduced flow of water through the animal. In some cases a few of the tubules were observed to be fully extended with open oscules and pores, while others of the colony were in various stages of contraction.

Upon prolonged exposure to lowered salinities, the tissue at the surface of the sponge colonies turned brown; this state usually (but not invariably) preceded failure of the colonies to resume normal activity within the period of observation. However, it is not certain whether such sponges were completely dead. In some cases, breaking open the shell revealed living sponge tissue within, which may have been capable of forming restitution bodies which could re-establish the colony after the lapse of a sufficient amount of time in normal sea water.

Cliona colonies exposed to very low salinities (5 or 3 o/oo) and to fresh water manifested a characteristic response. The tubules contracted, in general, only partially, and the tissue turned a pale, whitish color. This condition probably resulted from a rupture of the myocytes before complete contraction was achieved.

The results of individual experiments are presented as histograms with the aid of a survival index which summarizes the physiological condition of the colonies at the time of observation. Four categories of survival have been designated as follows:

1. Colony inactive and seriously damaged. Tubules partly extended or completely contracted; oscules closed; color abnormal (brown or whitish).

2. Colony inactive. No flow of water through the sponge. Tubules partly extended or completely contracted; oscules closed; color yellow.

3. Colony functioning, but at a reduced level. At least some of the tubules extended or partly extended with some oscules and ostia open or partially open.

4. Colony functioning normally. Tubules extended; oscules and ostia open.

Considering first the experiments on *Cliona celata,* reference to the histograms (figs. 34 through 39) which summarize the results reveal that this species is able to function efficiently in waters with a salinity down to 20 o/oo. Exposure to salinities as low as 15 o/oo causes some injury, but the sponge colonies are capable of carrying on at a reduced level of activity even after a week of exposure to this lowered salt concentration (experiment 1D, fig. 36). In all cases complete recovery followed a period of several days in sea water. In experiment 1E, however, after a week of exposure to water of 15 o/oo, the colonies were inactive and failed to recover after four days in sea water (fig. 36).

A salinity of 10 o/oo is near the critical one for *Cliona celata.* In experiment 1D, the colonies were still functioning at a reduced rate after 18 hours and 24 hours of exposure to 10 o/oo. These same colonies ceased functioning after 42 hours of exposure and were irreparably damaged after 72 hours of exposure to

[1] Vosmaer (1933) describes separate incurrent and excurrent papillae.

the same salinity. In all other cases in series 1, exposure to a salinity of 10 o/oo (even for periods of two to six hours) led to cessation of activity in that environment, although recovery followed placement in sea water in the case of colonies which had been kept in the lowered concentration for no longer than 24 hours.

In order to investigate tolerances in the critical range for survival, several series of experiments were run using salinities ranging from 13 o/oo to fresh water. Series 2 consisted of four different exposures to salinities of 12, 9, 6, and 3 o/oo; series 3 involved exposures to concentrations of 12, 9, 7.5, and 3 o/oo; in series 4, colonies were placed in salinities of 13, 10, 5, and 3 o/oo and in fresh water. These experiments were carried out from September to December when the water temperatures were decreasing steadily (fig. 41). The results, therefore, are not strictly comparable to those of series 1 nor to one another.

In series 2, carried on in September when the water temperature was not appreciably lower than it was during series 1, the sponge colonies were generally inactive after one to 24 hours of exposure to the several lowered salinities (fig. 37). In a single instance partial functioning was recorded after 24 hours of exposure to 9 o/oo. In general, complete or partial recovery followed transference to sea water for several days, although sponges exposed to 3 o/oo for four hours failed to resume a functional state after eight days in sea water, and colonies which had been in concentrations of 6 and 3 o/oo for 24 hours also failed to recover in sea water.

Series 3 was carried on in late October and early November, and results were similar to those of the previous series. In no case was there evidence of water currents flowing through the sponge colonies after periods of one to 96 hours of exposure to salinities of 12, 9, 7.5, and 3 o/oo (figs. 38, 39). Complete recovery followed removal to sea water after one, two, or four hours of exposure to the lowered salinities and after 24 hours in salinities of 12 o/oo and 9 o/oo. In the case of those colonies which were exposed to 7.5 and 3 o/oo for 24 hours, some of the colonies recovered; others did not (three out of six in 7.5 o/oo; two out of six in 3 o/oo).

The lower temperatures under which the experiments in series 4 were carried out produced a noticeable effect on survival. Experiments 4A and 4B (fig. 39) are comparable to 3E in regard to length of exposure, and it is evident that in the former instances some of the colonies remained active after being in the lowered salinities for 42 and 48 hours. Similarly, recovery in sea water was greater in series 4. The effect of lowered temperatures in increasing tolerances to lowered salinities in *Cliona celata* is shown strikingly in figure 42 where mean survival values after exposure and recovery in sea water are compared at 19° C. and 12.9° C.

Tables 37 to 40 summarize the data of the salinity experiments on *Cliona celata* and indicate along with figure 39 (series 4) the dependency of tolerance to lowered salinities upon (1) length of exposure to the diluted concentrations and (2) temperature.

Series 5 includes three experiments on the salinity tolerances of colonies of *Cliona vastifica* (fig. 40). After 96 hours of exposure (5C) to salinities varying from 27 o/oo to fresh water, complete recovery was noted after a week in sea water for individuals exposed to salinities of 20 o/oo. Those which had been immersed in water with a salinity value of 15 o/oo were not functional after a week in sea water, but showed normal tissue within, so that eventual recovery

was probable. Those exposed to still lower salinities failed to show any signs of recovery. In two sets of experiments (5A, 5B) carried on in the late fall, a surprisingly high percentage of colonies survived exposure to even the lowest salinities.

TABLE 37

SURVIVAL OF *CLIONA CELATA* AFTER VARYING PERIODS OF EXPOSURE TO LOWERED SALINITIES—SERIES 1

EXP. NO.	DURATION OF EXPOSURE	NO. OF COLONIES	CONCENTRATION OF SEA WATER IN PARTS PER MILLE					
			27	20	15	10	5	0
1B	2 hrs.	3	4*	4*	3*	2*	2*	1*
1D	2 hrs.	3	4	4	3	2	2	2
1C	6 hrs.	3	4	4	2	1	1	1
1D	18 hrs.	3	4	4	3	3	1	1
1D	24 hrs.	3	4	4	3	3	1	1
1D	42 hrs.	2	4	4	3	2	2	1
1D	72 hrs.	2	4	4	3	1	1	1
1E	72 hrs.	3	4	4	4(1)** 2(2)	1	1	1
1D	7 days	1	4	4	3	1	1	1
1E	7 days	3	4	4	2(2) 1(1)	1	1	1

* Numbers in these columns refer to survival index.
** Numbers in parentheses refer to number of colonies at each survival index level.

TABLE 38

SURVIVAL OF *CLIONA CELATA* AFTER A 3-DAY PERIOD OF RECOVERY IN SEA WATER FOLLOWING VARYING EXPOSURES TO LOWERED SALINITIES
SERIES 1

EXP. NO.	DURATION OF ORIGINAL EXPOSURE	NO. OF COLONIES	CONCENTRATIONS OF SEA WATER IN PARTS PER MILLE					
			27	20	15	10	5	0
1A	1 hr.	3	4*	4*	4*	3*	3*(2)** 1(1)	3*(1) 1(2)
1B	2 hrs.	3	4	4	4	3	1	1
1C	6 hrs.	3	4	4	4	3	1	1
1D	24 hrs.	1	4	4	4	1	1	1
1D	72 hrs.	1	4	4	4	1	1	1
1D	7 days	1	4	4	4	1	1	1
1E	7 days	3	4	4	1	1	1	1

* Numbers in these columns refer to survival index.
** Numbers in parentheses refer to number of colonies at each survival index level.

TABLE 39

SURVIVAL OF *CLIONA CELATA* AFTER VARYING PERIODS OF EXPOSURE TO LOWERED SALINITIES AND AFTER RECOVERY IN SEA WATER FOR A 3-DAY PERIOD—SERIES 2

EXP. NO.	DURATION OF EXPOSURE	NUMBER OF COLONIES	CONCENTRATIONS OF SEA WATER IN PARTS PER MILLE							
			12		9		6		3	
			Expos.	Recov.	Expos.	Recov.	Expos.	Recov.	Expos.	Recov.
2A	1 hr.	2	2*	3*	2*	3*(1)** 2(1)	2*	4*(1) 2(1)	2*	3*(1) 2(1)
2B	2 hrs.	2	2	4	2	4(1) 3(1)	2	3	1	4(1) 3(1)
2C	4 hrs.	2	1	4	1	3	1	3	1	1
2D	24 hrs.	2	2	3(1) 2(1)	3(1) 1(1)	4(1) 1(1)	1	1	1	2(1) 1(1)

* Numbers in these columns refer to survival index.
** Numbers in parentheses refer to number of colonies at each survival index level.

TABLE 40

SURVIVAL OF *CLIONA CELATA* AFTER VARYING PERIODS OF EXPOSURE TO LOWERED SALINITIES AND AFTER RECOVERY IN SEA WATER FOR A 3-DAY PERIOD—SERIES 3

EXP. NO.	DURATION OF EXPOSURE	NUMBER OF COLONIES	CONCENTRATIONS OF SEA WATER IN PARTS PER MILLE							
			12		9		7.5		3	
			Expos.	Recov.	Expos.	Recov.	Expos.	Recov.	Expos.	Recov.
3A	1 hr.	6	2*	4*	2*	4*	1*	4*	1*	4*(4)** 3(1) 1(1)
3B	2 hrs.	6	2	4	2	4	1	4	1	4
3C	4 hrs.	6	1	4(5) 3(1)	1	4	1	4	1	4
3D	24 hrs.	6	1	4	1	4(4) 3(2)	1	3(3) 1(3)	1	4(1) 3(1) 1(4)
3E	41 hrs.	6	2(3) 1(3)	2(2)† 1(2)	2(1) 1(5)	1	1	1	1	1
3E	96 hrs.	2	1	1	1	2(1) 1(1)	1	1	1	1

* Numbers in these columns refer to survival index.
** Numbers in parentheses refer to number of colonies at each survival index level.
† Recovery of four colonies followed; other two allowed to remain in water of lowered salinity for 96 hours.

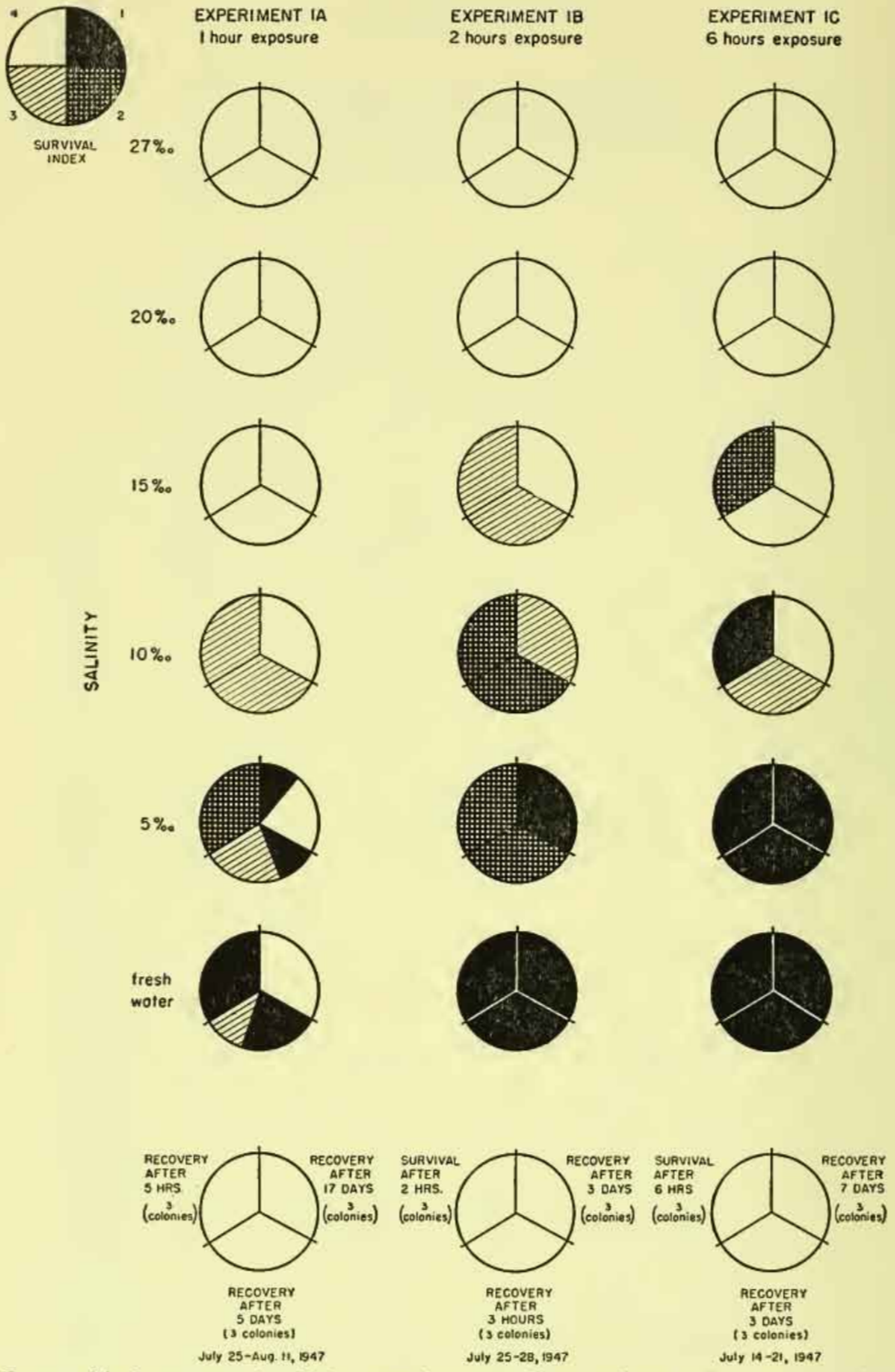


FIGURE 34. Summary of salinity experiments. *Gliona celata,* Series 1A, 1B, 1C. Survival index explained in text, p. 108.

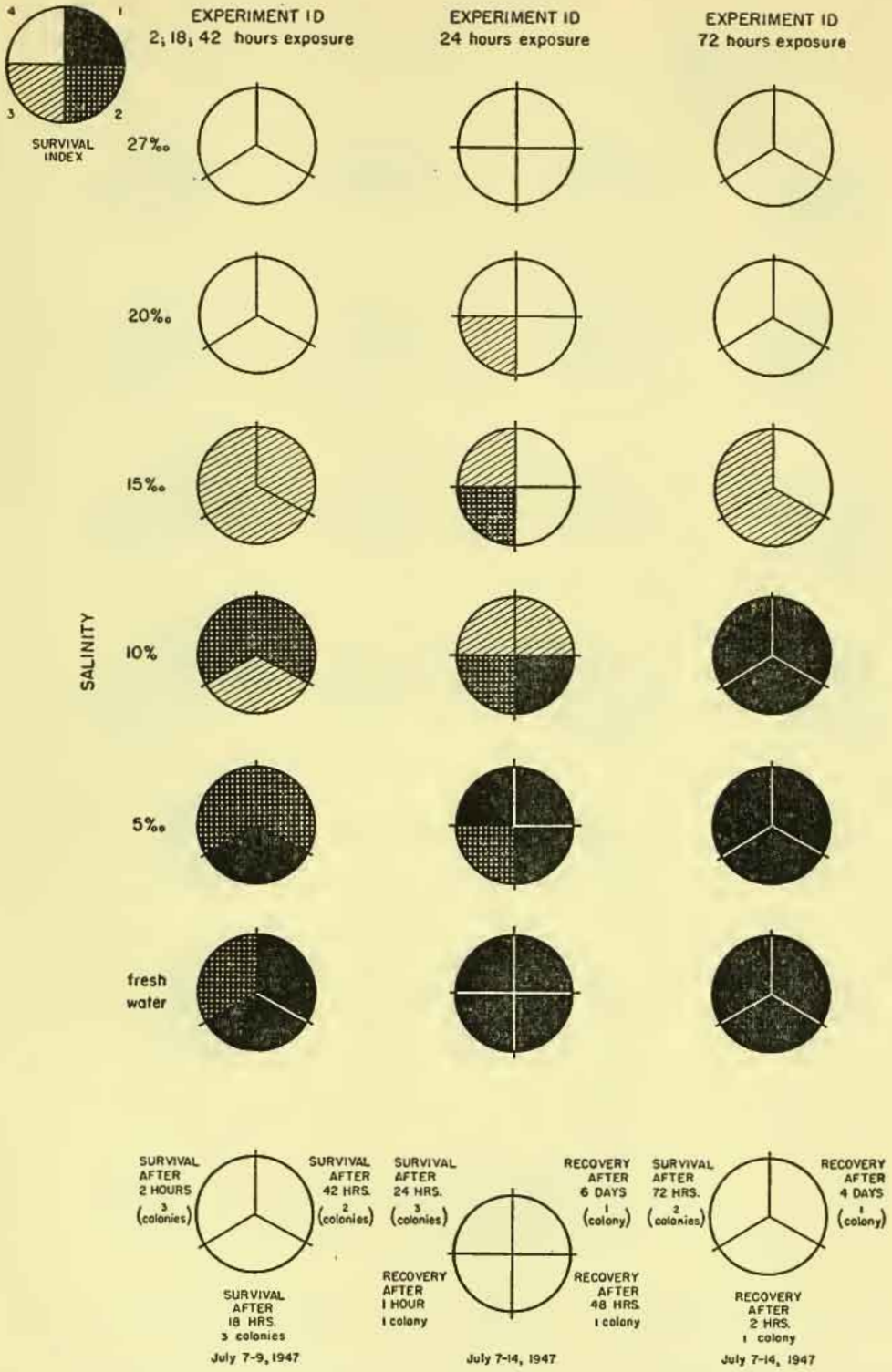


FIGURE 35. Summary of salinity experiments. *Cliona celata,* Series 1D.

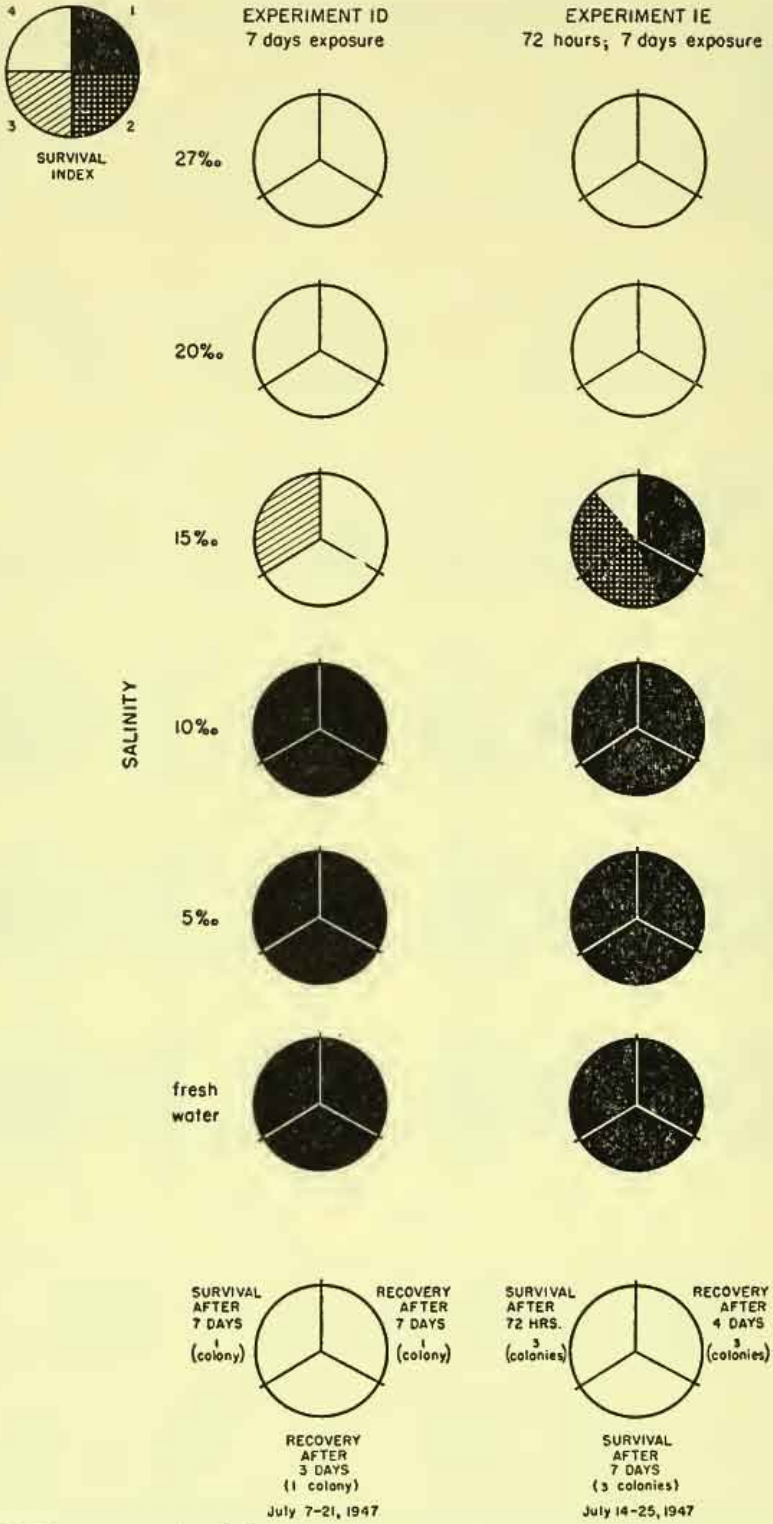


FIGURE 36. Summary of salinity experiments. *Cliona celata,* Series 1D, 1E.

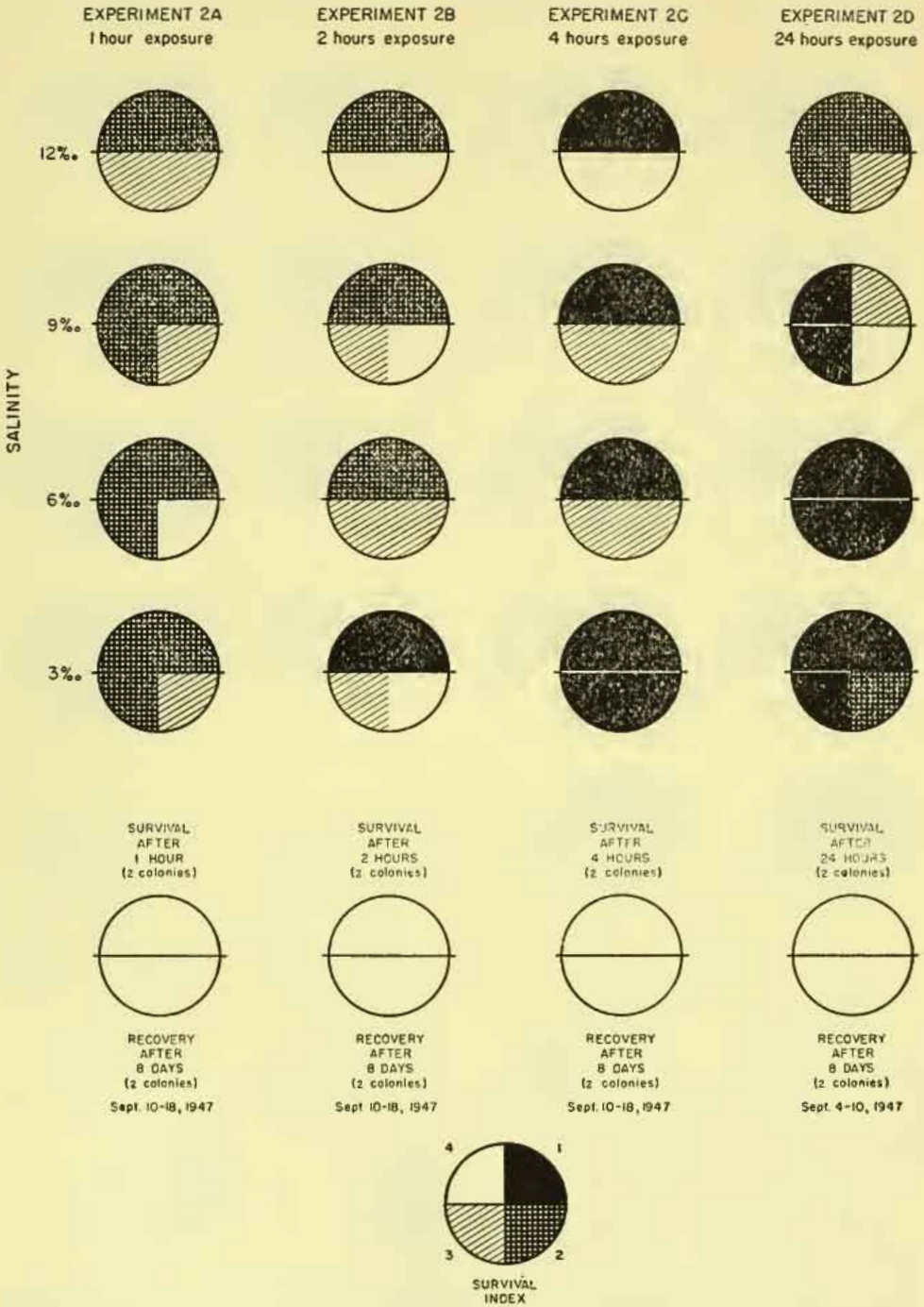


FIGURE 37. Summary of salinity experiments. *Cliona celata,* Series 2A through 2D.

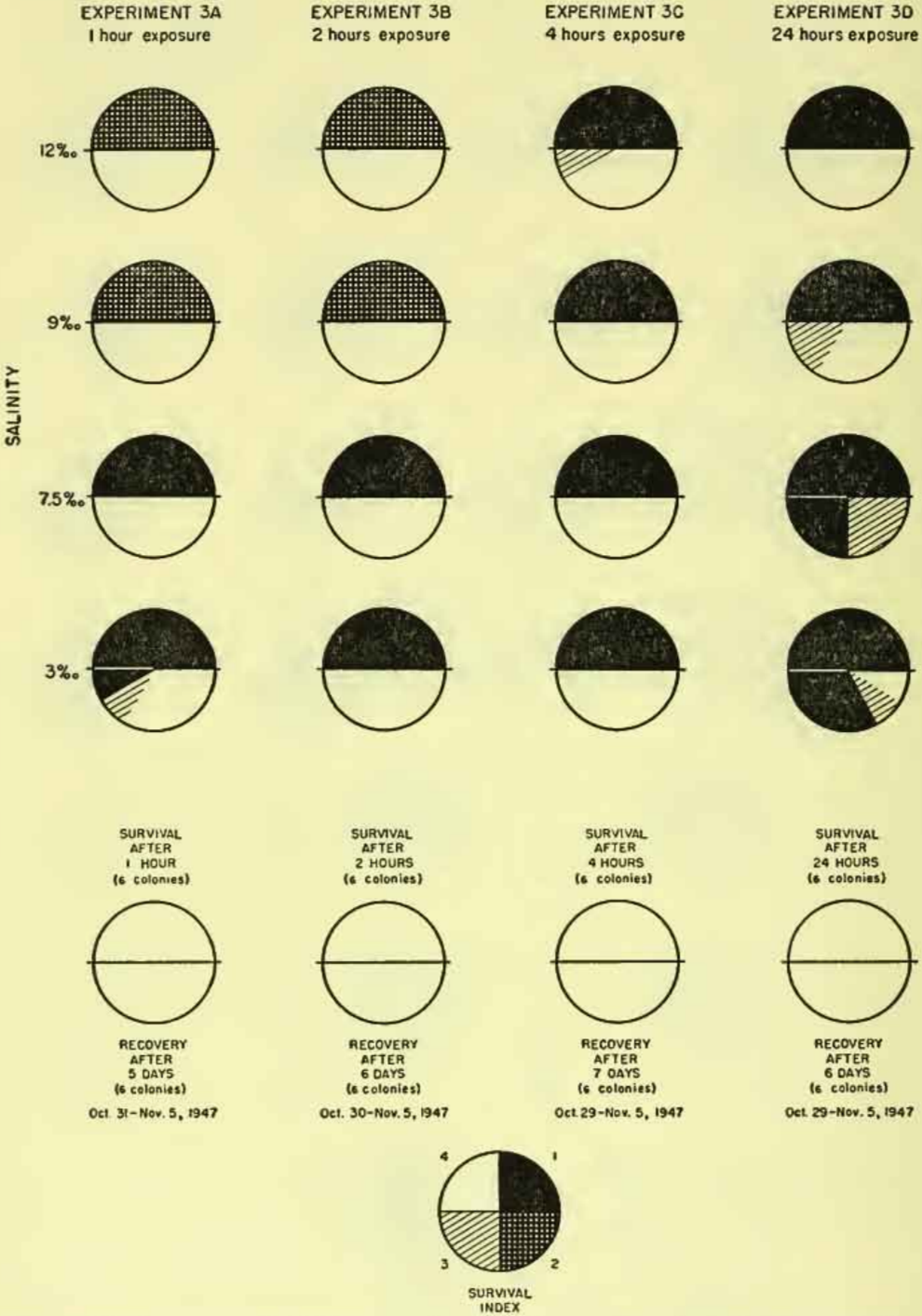


FIGURE 38. Summary of salinity experiments. *Cliona celata,* Series 3A through 3D.

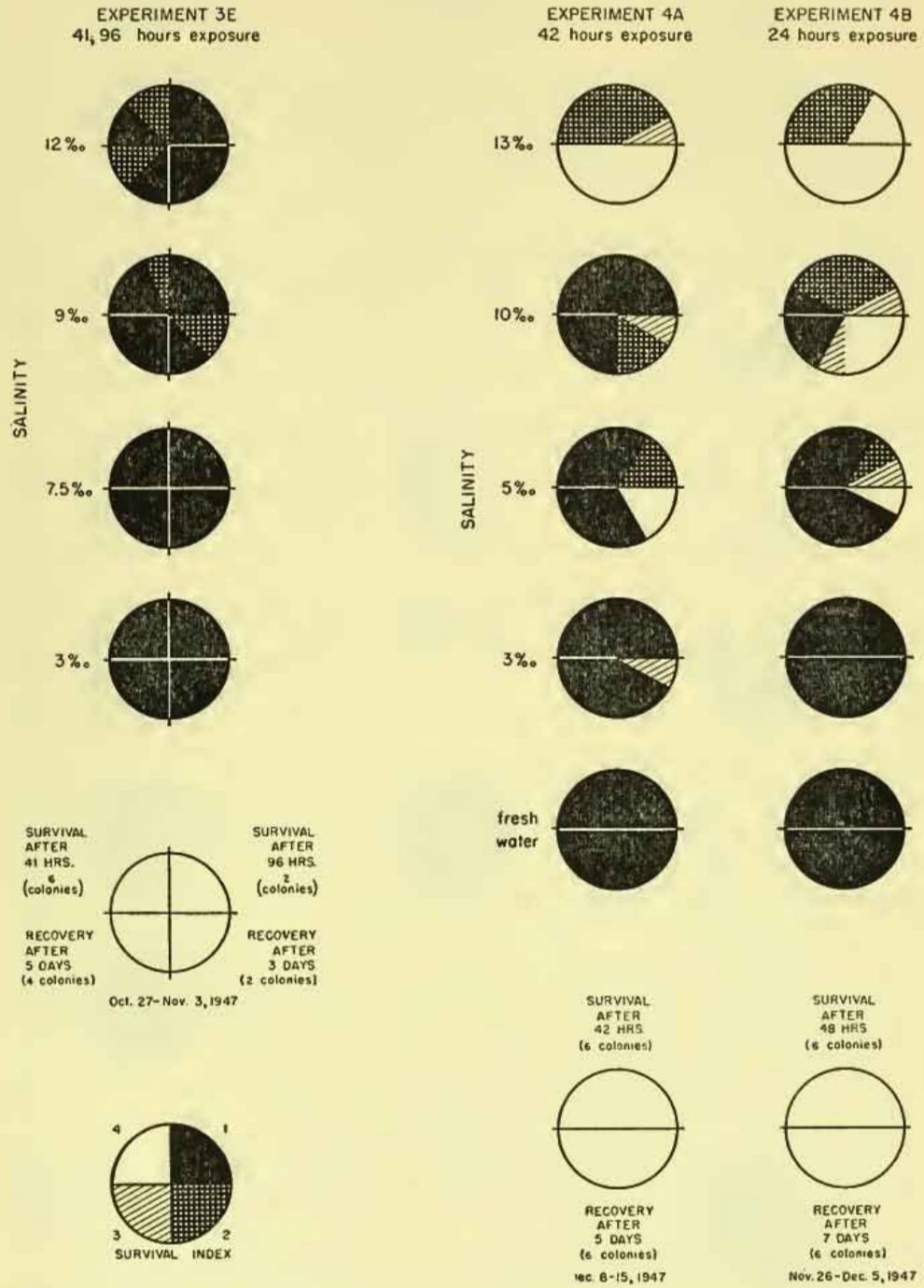


FIGURE 39. Summary of salinity experiments. *Cliona celata*, Series 3E, 4A, 4B.

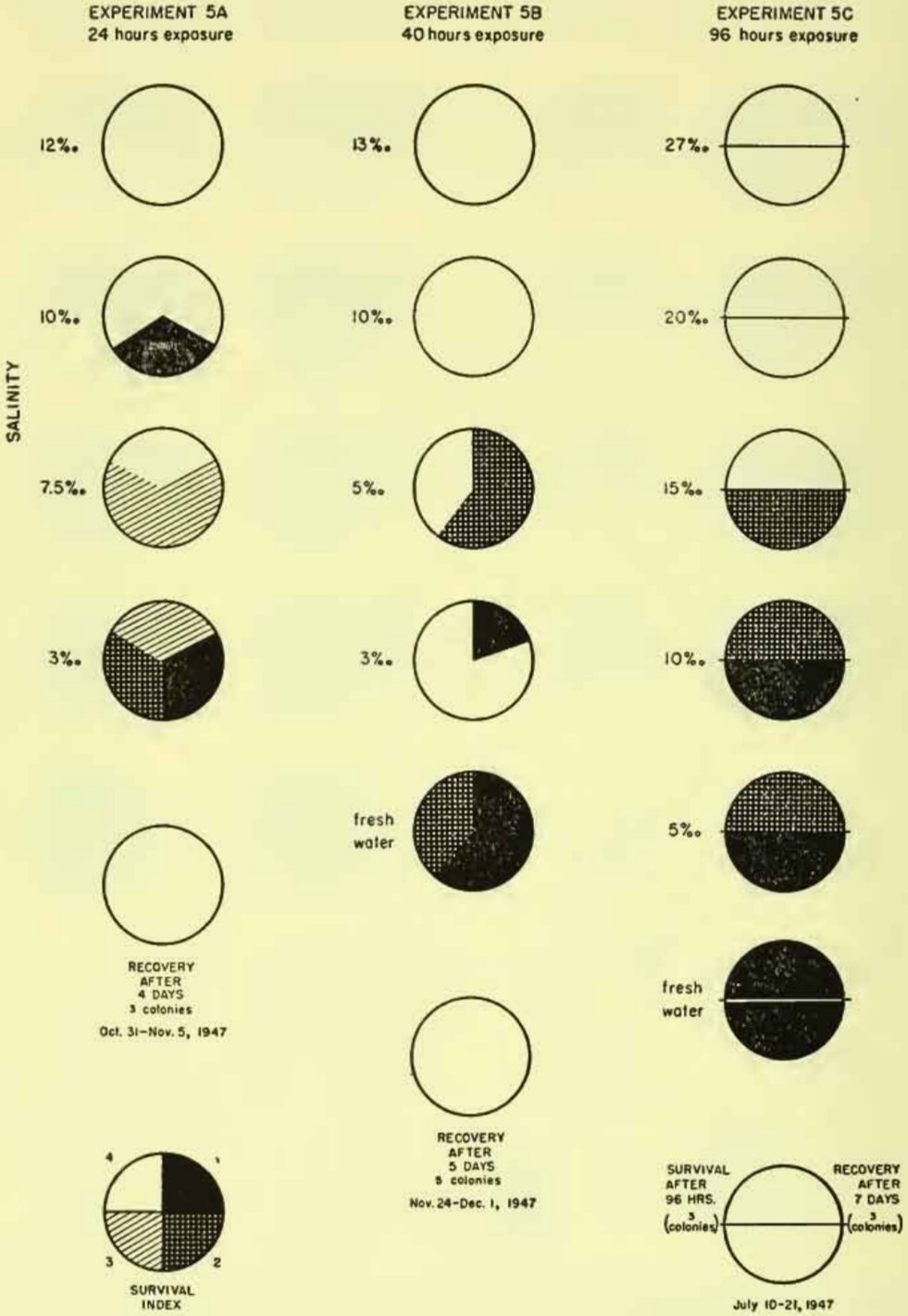


FIGURE 40. Summary of salinity experiments. *Cliona vastifica*, Series 5A, 5B, 5C.

DISCUSSION

OSMOREGULATION: An examination of the salinity determinations made twice weekly during the year of 1947 at the Milford Biological Laboratory indicates that variations in the salt concentrations of the bottom waters of Milford Harbor were slight, ranging from 23.5 o/oo to 29 o/oo. The lowest records were made following heavy rains, while the highest were recorded in late summer; the mean is near 27 o/oo. Surface salinities show a much wider range of values, varying from 5.2 o/oo after heavy rains to 29 o/oo in late summer. At an intermediate depth (three feet from the bottom in water six feet deep at mean low water) the lowest salinity recorded over the course of a year was 12.2 o/oo. All these records were made off the dock of the Milford Laboratory in water six feet in depth at mean low water level and about 30 feet from shore line at the same water level.

It is probable, therefore, that sponges inhabiting the bottom waters of Milford Harbor will seldom, if ever, come in contact with concentrations below 20 o/oo; so that the observations on salinity tolerances made in these experiments suggest that the sponge colonies have wider tolerances than are likely to be met with under natural conditions.

A capacity to adapt to wide changes in salinity may involve either (1) an active regulation of osmotic pressure within the body which serves to insulate the tissues from the salinity changes in the environment or (2) a wide tolerance to changes in the osmotic pressure of the body fluids, with little regulative capacity. Within any one phylum of invertebrates both conditions together with intermediates may occur, so that a clear-cut differentiation into homoiosmotic and poikilosmotic forms is impossible.

Since sponges have no body fluids, osmoregulation, if it exists, must be intracellular; and a similarity to conditions in protozoans might be expected. Jepps (1947) has shown that fresh-water sponges (genera *Spongilla* and *Ephydatia*) possess contractile vacuoles. Zeuthen (1939) found that the osmotic concentration of the cells of *Spongilla* rises three- to fourfold at the time of gemmulation. Although Jepps examined a variety of marine sponges, she was unable to find unequivocal evidence for the presence of contractile vacuoles in these forms. In one case, however, *Anchinoe* (= *Microciona*) *fictitia*, clear fluid vacuoles were observed in choanocytes. One such vacuole was seen to move forward during the period of observation until it came to lie within the base of the collar, in the position of the contractile vacuoles of the Spongillidae. Granule-containing vacuoles were also observed moving in choanocytes, but in no case was either type of vacuole seen contracting or discharging its contents. Although these vacuoles may not have been rhythmically contractile, it is not unlikely that they do serve to regulate water output. Kitching (1939) has pointed out that although marine rhizopods lack contractile vacuoles, excess water introduced by food particles is eliminated in food vacuoles. The vacuoles observed by Jepps in *Anchinoe* might well function similarly.

True contractile vacuoles were reported in the choanocytes of *Leucosolenia* by James-Clark (1868a, 1868b), but Jepps was unable to confirm these interesting observations in her study of the same genus. Saville Kent (1880-82) figured contractile vacuoles in *Grantia compressa* Bow., *Leucosolenia coriacea* Bow., and *Halisarca dujardini* Johnston; however, he gave no statement in his text which indicated that he had seen these structures functioning.

It may be suggested that sponges have been enabled to invade fresh waters by virtue of the presence of contractile vacuoles which probably function as in certain protozoans, as osmoregulatory mechanisms. The question of the possible function of vacuoles in water relations in marine sponges which have succeeded in entering brackish water remains to be further investigated. In marine sponges without vacuoles it seems likely that extension of range in brackish waters depends upon the tolerance of dilution of the internal milieu of the cellular elements, as in the few coelenterates which have been studied. Concerning the coelenterates, Bateman (1932) has critically reviewed the evidence for osmoregulation in the Scyphozoa and has presented work of his own showing that osmoregulation does not exist in these forms, the concentration of salts in the tissues varying directly with the external milieu. Palmhert (1933) studied the marine hydroid, *Clava multicornis* (Forskål) and found no evidence for active osmoregulation. Exposure to lowered salinities (down to 8–12 o/oo) resulted in an initial swelling of the polyps followed by a slow return to normal size. Death followed 48 hours of exposure to tap or pond water. Specimens placed in dilutions of sea water showed a decreased oxygen consumption, another indication of an absence of osmoregulatory mechanisms. Miyawaki (1951) suggests that secreted mucus plays a role in the resistance of actinians to low salinity. He found that *Diadumene luciae* (Verrill) survived in sea water diluted to 7.5 per cent.

In multicellular animals with a body fluid, the environment of the tissue cells can be regulated more readily. It has been shown by Wells and Ledingham (1940) that the rate of dilution is the determining factor in the sensitivity of isolated polychaete muscle tissue to diluted sea water. Beadle (1937) demonstrated that the tissues of intact polychaetes are protected from the effects of sudden dilution of the sea water by a "damping" of the body fluid dilution curve to the extent required for normal muscle functioning.

In a sense, a similar damping of the dilution curve of water in the canals of a sponge could be brought about by the closure of the ostia and oscules by which means a concentration of water higher than that in the environment would be maintained in the channels of the sponge colony. Parker (1910), in his classical experiments on the physiology of *Stylotella* (= *Hymeniacidon*) *heliophila,* found that diluted sea water induced merely a partial and imperfect contraction of ostia and oscules so that the internal cells were exposed to the lowered salinities and activity ceased in dilutions of 50 per cent or lower after a period of 10–12 minutes. He also showed that upon exposure to fresh water, ostial and oscular movements are paralyzed, and water currents cease immediately. Even after 24 minutes of such treatment, recovery occurs upon removal to sea water, the damaged choanocytes being restored after several days.

In the present studies of *Cliona* a complete contraction of the oscules was effected in the intermediate or critical salinities; that is, in salinities between those in which some activity occurred (27–20 o/oo) and those in which immediate damage to the cells took place (5 o/oo—fresh water). This critical range of salinities lies between 15 and 10 o/oo, and it is probable that a damping mechanism analogous to that observed by Beadle may help sponges through limited periods of exposure to these salinities through maintenance of a higher concentration of internal water. Since most exposures of bottom-dwelling sponges to fresh water under natural conditions (such as might occur after heavy storms at inshore areas) would be preceded by a gradual lowering of the salinity, it is probable that the sponge colonies would be completely contracted and thus pro-

tected before the harmful concentrations are reached. Parker, however, found that dilutions of sea water caused a relaxation of the ostia and oscules in *Hymeniacidon* (*Stylotella*) if these structures were closed before placement in the lower salinities; further investigations are needed to determine the extent to which the oscules and ostia may function in protecting sponges from lower salinities.

TEMPERATURE AND SALINITY TOLERANCE IN *Cliona celata:* In the investigations of *Cliona celata,* experiments carried out under different temperature conditions show distinctly different tolerances to diluted sea water. Figure 42 compares the results of two comparable experiments. The mean survival and recovery values for each concentration of diluted sea water are plotted for each temperature. In experiment 3E, carried out in late October at temperatures averaging 19° C.,

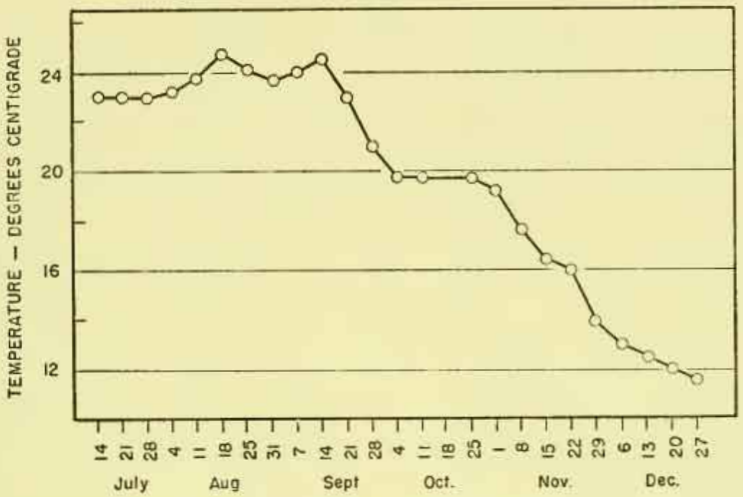


FIGURE 41. Water temperatures recorded during the salinity experiments. Each point represents a weekly mean of the averages of fresh and sea water temperatures.

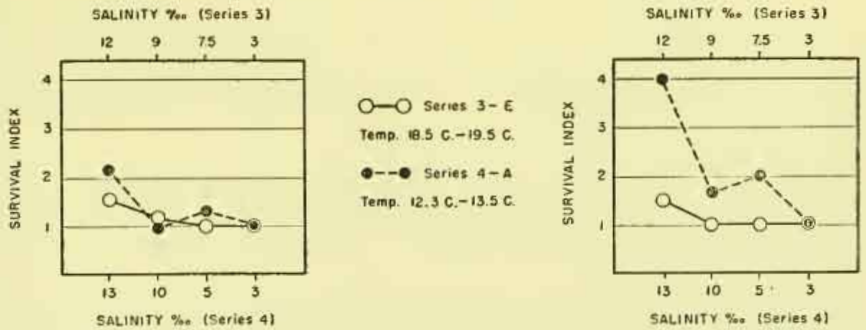


FIGURE 42. Effect of temperature on tolerance to lowered salinities in *Cliona celata.* Left, after 41 hours exposure to lowered salinities; right, after five-day recovery period in sea water following the above exposures to lowered salinities.

the mean survival index after exposure varies from 1.5 to 1.0 and shows a similar variation after "recovery." In experiment 4A, carried out in late November when temperatures averaged 12.9° C., the survival indices for recovery vary from 4.0 to 1.0, being from two to three times higher than in the previous experiment except at a concentration of 3 o/oo, which was lethal in both cases.

These observations are in keeping with expectations since tolerance to reduced salinities involves physicochemical processes such as diffusion and permeability. Lucké and McCutcheon (1932), e.g., found a high effect of temperature on the permeability of unfertilized sea urchin eggs, both in endosmosis and exosmosis. They accounted for their observations in terms of changes in the viscosity of water and in the permeability of the cell surface.

SALINITY TOLERANCE AS A FACTOR IN THE DISTRIBUTION AND SPECIATION IN THE GENUS *Cliona:* When the experimentally determined tolerances of *Cliona celata* and *Cliona vastifica* to reduced salinities are compared, the latter species is seen to have a distinctly wider range of tolerance to this factor. Figure 43 shows the percentage survival values of colonies of the two species after a 24 hour period of exposure to a series of salinities varying from 12 o/oo to 3 o/oo, followed by a recovery period of several days in sea water. The criteria for survival used were (1) presence of open oscules with water currents issuing from them or (2) in the event that all oscules were closed, survival was considered certain if the color of the tissue was normal and if piles of shell chips could be detected at the base of one or more of the oscules. Figure 43 also compares percentage survival values of colonies of *Cliona celata* after recovery from 42 hours of exposure to salinities varying from 13 o/oo to fresh water, with survival values of *Cliona vastifica* after recovering from 40 hours of exposure to the same series of low salinities.

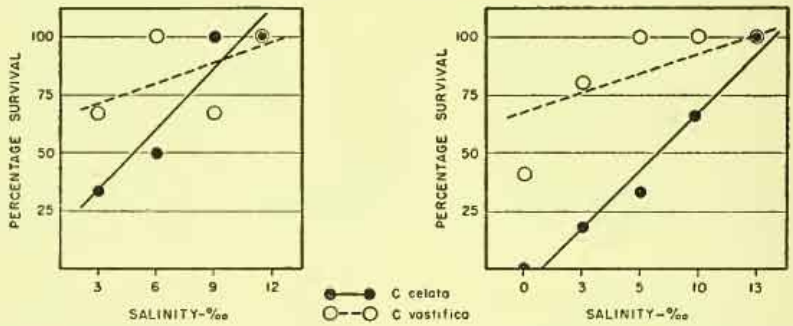


FIGURE 43. Comparative tolerance to lowered salinities of *Cliona celata* and *C. vastifica*. Left, after 24 hours of exposure to lowered salinities; right, after 40 hours of exposure to lowered salinities.

In the case of both sets of data (24 hours and 40 hours of exposure respectively) straight lines have been fitted to the points by the method of least squares. The regression coefficients for the two species in each case differ significantly at a level lower than one per cent.

This experimental evidence suggests that salinity tolerance may play a role in determining the distribution of these two species and that salinity may have operated as an isolating factor in speciation.

A consideration of the world-wide occurrence of the two species of *Cliona* concerned reveals that their distributions overlap in large areas, and that the

relative abundance of the two species varies considerably. *Cliona vastifica* occupies a greater variety of habitats, ranging from low water neap tides to depths of 600 meters. It is also found consistently in waters of reduced salinity where *Cliona celata* is excluded. The latter species ranges from mean low water to depths of 200 meters (rarely). Further consideration of the general distribution of these two species with a discussion of competition between them will be found in a later section. For the present, the occurrence of these species in brackish waters will be treated specifically.

The limitations placed upon the distribution of *C. celata* and *C. vastifica* by reduced salinity are parallel over a large part of their range: both occur in the mouth of the Chesapeake Bay, in Beaufort Harbor, in Long Island Sound, in the Belt Seas of Denmark, in the Étang de Thau. In Louisiana the data of Hopkins (1956a) indicate that *C. celata* is found farther up estuaries than is *vastifica;* however, only three colonies of the latter species (2 per cent of all clionids identified) were found during his studies. None were recorded from waters of higher salinity (his zone 5). In South Carolina, too, Hopkins (1956b) found that *vastifica* makes up a relatively small proportion of the total clionid population (9.5 per cent of all boring sponges identified, as compared to *celata* which comprises 74 per cent of the total). *C. celata,* alone, was found at station 4 (South Santee River) where the lowest salinity (16.6 o/oo) of his survey was recorded. A salinity of 26 o/oo was the lowest observed at stations where *C. vastifica* was found. The salinity records of Hopkins' South Carolina survey have a limited significance, however, since they represent single determinations in most instances.

One striking fact stands out in reviewing the distribution of *Cliona vastifica.* Populations which seem to bear a close relationship to *vastifica* in morphological traits have penetrated into brackish (mesohaline) waters in four regions of the world: the Atlantic and Gulf coasts of North America, the Oued Melah, the Black Sea, and Chilka Lake. The first form, which is sufficiently differentiated from *C. vastifica* to merit specific rank, has been named *C. truitti*[2] by Old (1941). The seaward limit of its range in Chesapeake Bay occurs in a region where the surface isohalines show an annual range of 15 to 17 o/oo and the annual range of salinities at 20 meters is 14 to 20 o/oo (Cowles, 1931). The extension of its range into the headwaters of the bay includes waters with a surface salinity down to 6 o/oo and an annual range at 20 meters of 10 to 16 o/oo. It occupies a region approximately equivalent to Valikangas' pleiomesohaline zone. The boundary between the area inhabited by *C. truitti* and that occupied by *C. vastifica* and *C. celata* is very sharp according to Old's data (fig. 44).

Hopkins (1956a, 1956b) has studied the distribution of *Cliona truitti* on the coasts of Louisiana and South Carolina and has presented excellent salinity data for the waters where collections were made in the former locality. Hopkins has used the clionids as "salinity indicators" and has attempted to classify the estuarine waters of Louisiana into six "*Cliona* zones." His observations show that the range of *C. truitti* in Louisiana overlaps those of *celata, vastifica,* and *lobata* (see Table 41), unlike the distribution patterns given by Old for Chesapeake Bay. Only in Hopkins' zone 1, with annual salinity range and mean values of 1–*11*–25 o/oo, and with salinities below 5 o/oo recorded on 15 per cent of the days of the year, does *Cliona truitti* occur to the exclusion of all other clionids. *Cliona celata* is found along with *truitti* in zones 2 through 5.

[2] Old also reports *C. truitti* from Long Island Sound but gives no exact locality. It would be of interest to know whether it is restricted to brackish water bays there.

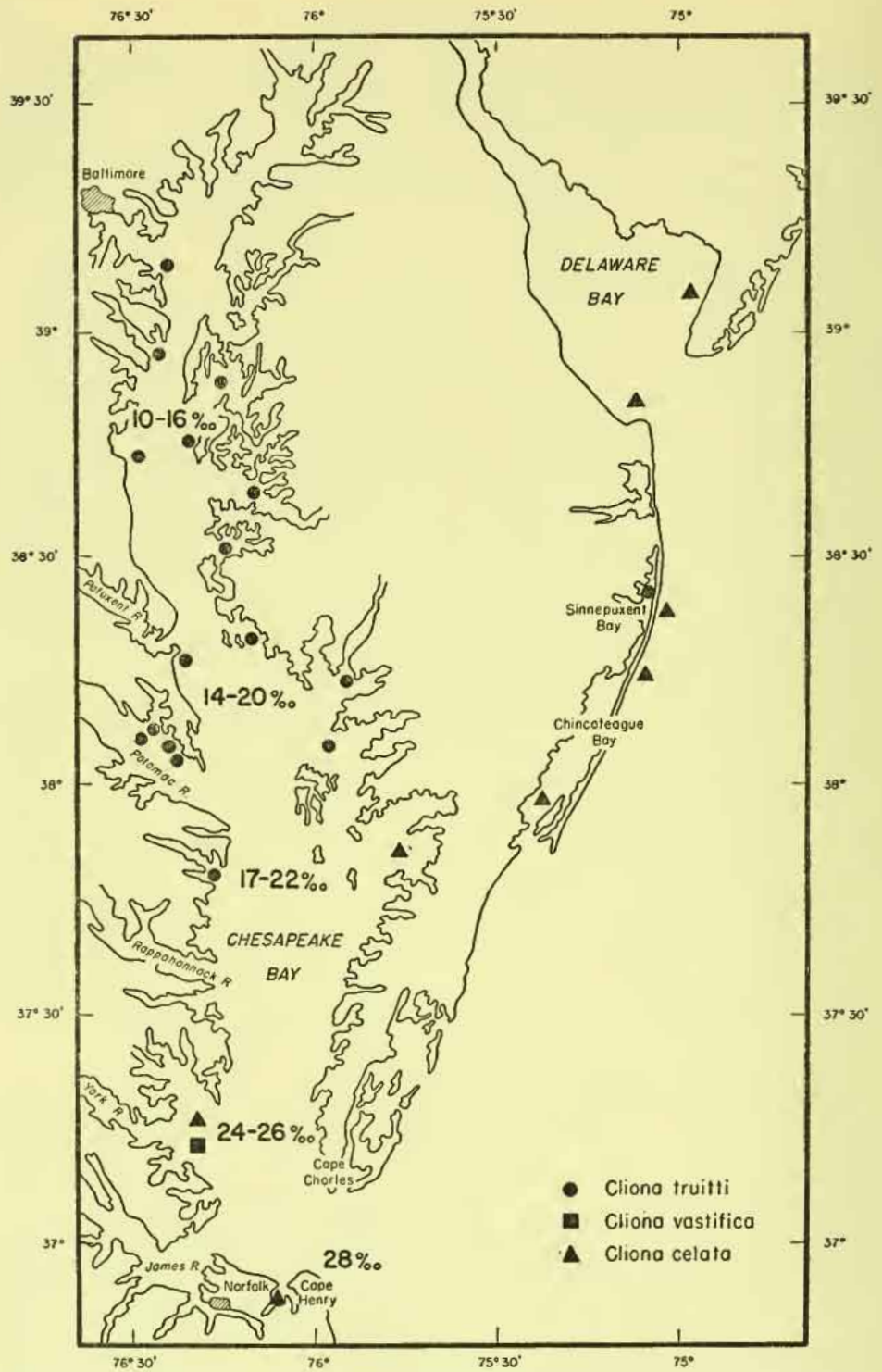


FIGURE 44. Distribution of clionids in the Chesapeake Bay region in relation to salinity.

TABLE 41

DISTRIBUTION OF CLIONIDS IN LOUISIANA IN RELATION TO SALINITY
(Data compiled from Hopkins, 1956a)

ZONE NO.	1	2	3	4	4	5
LOCALITY	BAY CHENE FLEUR	BAYOU BAS BLEU	LOWER BARATARIA BAY	BAY STE. ELAINE	LAKE BARRE	CAILLOU ISLAND
Range and mean salinity values for a one-year period*	1–*11*–25 o/oo	6–*15*–25 o/oo	1–*22*–30+ o/oo	10–*21*–30 o/oo	10–*23*–30 o/oo	No data given
Per cent of days below 5 o/oo	15	0	1.5	0	0	0
Per cent of days below 10 o/oo	46	4	6	0	0	0
Per cent of days below 15 o/oo	76	32	10	2	1.5	0
Per cent of days below 20 o/oo	98	73	35	37	25.5	Seldom
NUMBER OF SPECIMENS IDENTIFIED						
C. celata	0	Relatively scarce	8	8	7	7
C. vastifica	0	0	0	2	1	0
C. truitti	2	Abundant	26	9	10	2
C. lobata	0	0	1	4	1	0

* Based on Table 4, Hopkins (1956a), in which the percentage of days in a one year period which fall in each of seven salinity ranges are compared.

Hopkins' South Carolina studies (1956b) are of great interest. An accumulated rainfall deficiency of about 47 inches in the last seven years combined to a lesser extent with a recent rise in sea level in that area have led to an increased salinity in the estuaries. "Sea water had replaced brackish water of low salinity in most of the estuaries; water of almost oceanic salinity was found even in small creeks far inland." Where possible, salinity data recorded by Lunz during a survey of coastal waters of South Carolina in 1935 (reported by Hopkins, 1956b) are compared with the 1956 salinity records of Hopkins in Table 42. Although based in all cases

TABLE 42

SALINITY RECORDS IN SOUTH CAROLINA ESTUARIES IN 1935 AND 1956

LOCALITY	SALINITY IN 1935 (LUNZ)	SALINITY IN 1956 (HOPKINS)
Rantowles Creek	9.1 o/oo	31 o/oo
Five Fathom Creek (mouth)	14.0, 17.8, 19.7 o/oo	30.6 o/oo
Wadmalaw River	19.1, 20.0, 21.5 o/oo	32 o/oo
Fish Creek (mouth at St. Helena Sd.)	32.6 o/oo	32 o/oo (middle of St. Helena Sd.)
Ashepoo River	25.6, 27.0, 29.6 o/oo	29 o/oo (1–4 mi. above 1935 record)
Mackay and Skull Creek	26.9, 28.7, 29.3 o/oo	26.2–31.2 o/oo (1955)

on single salinity determinations these data give some idea of the magnitude of the changes in salinity which have occurred at some stations.

In regard to the distribution of clionids in South Carolina, Hopkins found that *C. truitti* is relatively much less abundant there than in Louisiana. In South Carolina *truitti* comprised 10 per cent of the 1527 boring sponges identified by Hopkins, whereas 73 per cent of the 148 specimens identified in Louisiana were *truitti*. These facts suggest that the invasion of South Carolina estuaries with water of higher salinity is resulting in a replacement of *Cliona truitti* by the other three species of *Cliona* found there. This conclusion is borne out especially well by the data from Rantowles Creek, in which 1950 and 1956 collections are compared (Table 43). Salinity records for Rantowles Creek in 1950 are not given, but available data indicate a sharp rise in salinity since 1935: 9.1 o/oo, 1935; 17.6 o/oo, 1955; 31.0 o/oo, 1956.

No experimental data are available as yet in regard to the tolerance of *C. truitti* to higher salinities. Thus it is difficult to say at present whether this species is dying back in South Carolina because it is unable to tolerate more saline waters which are moving up the estuaries or because of competition for substratum or food with the other clionids which are now able to live farther up the rivers.

TABLE 43

RELATIVE ABUNDANCE OF CLIONIDS AT RANTOWLES CREEK IN 1950 AND 1956

YEAR	NUMBER OF EACH SPECIES IDENTIFIED AND PER CENT OF TOTAL			
	Cliona celata	*Cliona truitti*	*Cliona vastifica*	*Cliona lobata*
1950	1 (11%)	8 (89%)	0	0
1956	49 (38%)	39 (30%)	4 (3%)	38 (29%)

Old's collections of *Cliona robusta* and *C. spirilla*[3] were made at Piver's Island, Beaufort Harbor, N. C., where salinity variations have been studied by Gutsell (1931). The ranges and means of the monthly maximum and minimum salinities as observed by Gutsell at Piver's Island over a four year period are 38–*33*–24 o/oo and 35–*25*–6 o/oo, respectively. The low reading of 6 o/oo was made after a heavy rain in September; minimum salinities of 14 to 20 o/oo are not infrequent in the late fall and winter months. De Laubenfels (1947) recorded salinities as low as 15 o/oo in July, 1946, during an exceptionally rainy summer. No information is available about the occurrence of clionids in Newport River where the salinity values are lower.

In the Black Sea the degree of difference of the local form (described as *C. stationis*) from typical specimens of *C. vastifica* as it occurs in the Mediterranean is not as great. The surface salinity of the Black Sea is 18 o/oo, increasing somewhat with depth (Nikitin, 1931), and it may be that the clionid population is not completely isolated from that of the Mediterranean proper. In Chilka Lake the local form is barely distinguishable from the typical open sea variety.

In all these cases the oxeas and spirasters are similarly modified in waters of lowered salinities, although the extent of modification varies greatly. The acanthoxeas tend to be longer and to possess central swellings, this characteristic being most pronounced in the case of *C. truitti*. This centrotylote condition is merely an intensification of a tendency present in *Cliona vastifica* in general. Many of the acanthoxeas in specimens of this species from Long Island Sound observed by the present writer have a trace of centrotylosis. The spirasters tend to be shorter in the brackish water forms and are, in general, less angulated than in typical specimens of *Cliona vastifica*. In addition to spicule differences, there is a noticeable enlargement of the sizes of oscular and ostial tubules in the case of *C. truitti* as compared with *C. vastifica*. Information in this regard is lacking for the other brackish water types.

Topsent (1932) has reported an abnormal variety of *Cliona vastifica* collected by Seurat in brackish water in the Oued Melah at Nador on the coast of Tunis. Specimens of the same species of sponge from a station in the open sea at nearby Skira show a typical structure. The tylostyles of the brackish water form are little modified. The diactinal megascleres are smooth oxeas, contrary to any other brackish water populations in the world; but these oxeas do tend to have a

[3] Hopkins (1956b) has found specimens in South Carolina intermediate between *Cliona spirilla* and *vastifica* and suggests that they may be conspecific.

central swelling, which seems to be a consistent development in all areas of greatly reduced salinity. The microscleres are noteworthy for their sparse spination, unusual thickness, and a tendency to be straight rather than spiral. A few of the microscleres are longer than the rest and tend to be pointed at one end as though they were intermediate between spirasters and oxeas. Czerniavsky (1880) described a species, *Cliona pontica* (from the Black Sea coast of the Caucasus at Sukhumi in water 1.5 to 15 meters deep) with smooth oxeas, many of which are figured as being centrotylote in form. No spirasters were found in these specimens. Nasonov (1925) was unable to find specimens fitting the description of *C. pontica* among Czerniavsky's collections from Sukhumi in the Zoological Museum of the Academy of Sciences of the U.S.S.R. He did find *Cliona lobata* in the shells of these collections, however. Nikitin (1934) recorded only *Cliona stationis* during the course of his survey of the Gudaut oyster bank near Sukhumi.

It is of interest to note in passing that microscleres seem to be more sensitive than megascleres to changes in the chemical conditions of the environment. This is obvious from the present information in regard to the influence of lowered salinity, and it was found to be equally true by Jewell (1935) and Jørgensen (1944) who raised fresh water sponges in water of reduced silicon content.

It would be instructive to acclimatize colonies of *Cliona vastifica* to waters of lowered salinities in order to determine whether modifications of the spicules such as are outlined above are environmentally induced. Similarly, *C. truitti* should be raised in waters of higher salinity to find out whether the modifications observed are genetically stabilized. Spicule sizes of the forms considered above are summarized in Table 44.

The experimentally demonstrated salinity tolerances of *C. celata* and *C. vastifica* reveal that both species are capable of functioning in environments with salinities lower than those ordinarily met with in their range of occurrence. Both are capable of withstanding very low salinities for short periods, a protective capacity necessary for any organism which penetrates inlets with variable salt concentrations. *C. vastifica* has been shown to possess the capacity of functioning in lower salinities than is true of *C. celata*. This, as will be apparent from the more detailed analysis of its geographical distribution, is merely another instance of its generally higher tolerance of environmental extremes. It is not surprising therefore, that *C. vastifica* should have an initial advantage under conditions of lowered salinity such as have led to the formation of *Cliona truitti* in Chesapeake Bay and of the brackish water populations of *C. vastifica* elsewhere in the world. It is strange that *C. vastifica* has not penetrated more deeply into the Baltic Sea; perhaps this fact is correlated with the restricted eastward range of *Ostrea edulis* although certainly other molluscs are available for colonization there. The fact that the Baltic has been connected with the North Sea for a relatively short time may explain the absence of a distinct population of *C. vastifica* there.

The gradation in differentiation of the brackish water populations of *Cliona vastifica* throughout the world is a matter of great interest. There is a range of variation from full species formation and probable reproductive isolation in Chesapeake Bay to subspecies formation in the Black Sea and incipient variation in Chilka Lake, and finally, to the complete absence of a brackish water population in the Baltic Sea. If adequate studies of the microfossils in the sediments of all these regions were available to provide information on the history of the salinity changes of these bodies of water, some concept of the time taken

TABLE 44

SPICULE SIZES OF *CLIONA VASTIFICA* AND RELATED FORMS

SPECIES	LOCALITY, AUTHOR	TYLOSTYLES L x W	ACANTHOXEAS L x W	SPIRASTERS L x W
Cliona vastifica	Atlantic Coast Old, 1941	160–150μ x 3–5μ	50–110μ x 2.5–4μ	6–23μ x 1–3.5μ
Cliona truitti	Chesapeake Bay Old, 1941	190–225μ x 5–3.5μ	110–130μ x 2.5–3.5μ	7–12μ x 0.5–2μ
Cliona vastifica	Rovigno Volz, 1939	280–306μ x 3.5–5.5μ	95–132μ x 3–4μ	11–16μ x 1.5–3μ
Cliona vastifica	Sevastopol Swartschewsky, 1905	168–340μ x 3–9μ	120–140μ x 2–3μ	8–12μ x 2μ
Cliona stationis	Sevastopol Nasonov, 1925	245–313μ x 5–7μ	75–175μ x 2.5–10μ (at center)	9–13μ
Cliona vastifica	Oued Melah, Tunis Topsent, 1932	260–290μ x 4μ (7.5μ at base)	(smooth oxeas) 55–110μ x 3–5μ	9–20μ, usually 12–15μ, x 2.5-4μ (some 30–40μ x 4μ)
Cliona robusta	Beaufort Harbor Old, 1941	160–200μ x 2–4μ	(spined or smooth oxeas) 40–130μ x 4–12μ	8–16μ x 1–2μ
Cliona spirilla	Beaufort Harbor Old, 1941	160–230μ x 2–4μ	80–170μ x 3–9μ	9–20μ x 1–2μ

for speciation under the differing conditions of temperature and availability of substratum could be obtained. More extensive biometric studies of the sponge populations in each case are also needed.

THE ZOOGEOGRAPHY OF *CLIONA CELATA, CLIONA VASTIFICA,* AND OTHER CLIONIDS

INTRODUCTION: Animals boring into calcareous matter, which is limited in amount in any environment, might be expected to be in strong competition for substratum. The substratum factor represents an area of overlap in the definition of the niches of all such animals in any one region. Differences in the ecology of such animals can be sought in feeding mechanisms, intrinsic growth rate, and breeding periods. The summary of the distributions of *Cliona celata* and *Cliona vastifica* given here, demonstrates that these species coexist over a large part of their range, but that one or the other of them is invariably more abun-

dant. All of the substratum available is probably never occupied; on Long Island Sound oyster beds, for instance, about 80 per cent of the oysters are infected with boring sponge colonies. Hopkins (1956b) found that 72 per cent of the 2116 shells which he examined in South Carolina were infected with clionids. Similarly it is doubtful if every available bit of substratum of the limestone cliffs of the Adriatic Sea is occupied. Nonetheless, it is apparent that a competitive relationship exists from the frequent occurrence of colonies of two species in the same oyster shell in the former locality and by the restricted and specialized substratum requirements exihibited by some of the species found in the latter region.

The number of species of clionids which coexist in any locality varies considerably as a function of the amount of substratum available, a fact which is apparent from Table 45. Warm limestone areas seem to be most favorable for

TABLE 45

OCCURRENCES OF CLIONIDAE ON DIFFERENT SUBSTRATA

LOCALITY	NUMBER OF SPECIES	DOMINANT SUBSTRATUM	AUTHOR
Rovigno d'Istria	9(3)*	Limestone	Volz, 1939
Beaufort, N. C.	5(2)	Oyster shells	Old, 1941
Chesapeake Bay	4(1)	Oyster shells	Old, 1941
Long Island Sound	4	Oyster shells	Old, 1941
West-central Pacific	5(1)	Dead coral	de Laubenfels, 1954
Bermuda	2(1)	Corals	de Laubenfels, 1950
Gulf of Maine (Deep water)	1	Scallop shells	Hartman

* Endemic species in parentheses.

the growth and speciation of clionids; brackish water oyster beds provide an abundance of substratum and favorable conditions for speciation. Coral reefs do not present as wide a variety of clionids as might be expected. De Laubenfels (1950, 1954) reports two species from Bermuda and five from the west-central Pacific. The latter species show little overlap in distribution, however. *Cliona lobata* Hancock and *C. vastifica* Hancock occupy distinct atolls in the Marshall Islands; *C. lobata* was also recorded from Truk and *C. euryphylla* Topsent from Ponapé in the eastern Carolines; *C. schmidti* (Ridley) was found in the Palaus; *Aka trachys* de Laubenfels is described by its author as possibly the only clionid in the Marianas. Burton (1934) reports no clionids from the Great Barrier Reef although he believes that two species of *Spirastrella* there may pass through a boring stage in early life.

DISTRIBUTION IN TEMPERATE REGIONS: A detailed tabulation of the occurrences

of *Cliona celata* and *Cliona vastifica* is unnecessary in the present work since both Vosmaer (1933) and Volz (1939) have recently compiled such records. Instead, attention will be focused on several well studied areas in an attempt to ascertain the limiting factors in the distribution of these two species.

Along the Atlantic Coast of North America, the distribution of these species has been studied by Lambe (1896), George and Wilson (1919), Procter (1933), Old (1941), de Laubenfels (1947, 1949), Hopkins (1956a, 1956b), and the present writer. *Cliona celata* occurs in inshore waters from Prince Edward Island to the coast of South Carolina, reaching its greatest abundance in waters of somewhat lowered salinity (30 to 25 o/oo) such as occur in coastal bays and sounds where oysters are cultivated extensively. This species is especially common in Malpeaque Bay (Prince Edward Island), Buzzard's Bay, Narragansett Bay, Long Island Sound, Delaware Bay, Chesapeake Bay (southern part), Beaufort Harbor (N. C.), and in the estuaries of the South Carolina coast. In the Gulf of Mexico it has been reported from St. George's Sound, Florida (Menzel, 1956), from oyster beds along the coast of Louisiana (as *Cliona sulphurea* by Moore, 1899, and Cary, 1906a, b; 1907a, b; also by Hopkins, 1956a), and has been identified by the present writer in oyster shells from Aransas Bay, Texas. Hopkins (1956a) also reports *celata* from Texas bays.

Cliona vastifica also ranges widely along the American Atlantic Coast. It has been collected by the present author in *Pecten magellanicus* shells in the Bay of Fundy (off Grand Manan Island, 30 meters), in a fragment of an unidentified mollusc in the Gulf of Maine (Fippennies Ledge, 80 meters), and in the shells of *Pecten magellanicus* in Massachusetts Bay (Stellwagen Banks, 40 meters). It is noticeably absent from inshore waters in northern areas. Procter (1933) failed to find *C. vastifica* in his survey of the Mt. Desert Island fauna, although *C. celata* is common there; de Laubenfels does not record it from Woods Hole where *C. celata* is again the common boring sponge. In Long Island Sound *Cliona vastifica* occurs along with *C. celata* on oyster beds. In the experience of the present writer, *C. celata* is about twice as common as *C. vastifica* on oysters near New Haven, Connecticut. The percentage of infection of *Crassostrea virginica* shells by boring sponges in a sample collected on an oyster bed off Woodmont, Connecticut, is given in Tables 46 and 47.

Old (1941) has recorded *C. vastifica* from the southern shores of Long Island Sound but has given no indication of its abundance relative to *C. celata*. *C. vastifica* was also found by Old in York River, Chesapeake Bay, and in Beaufort Harbor, N. C. Lunz (1935) and Hopkins (1956b) recorded it on oyster beds along the South Carolina coast where it made up 9.5 per cent of all clionids examined by Hopkins. Careful search would probably reveal its presence in Delaware Bay, Narragansett Bay, and Buzzard's Bay. Pearse and Wharton (1938) listed it from Apalachicola Bay, Florida; Hopkins (1956a) recorded it from Louisiana where it comprised 2 per cent of clionids identified.

Thus *Cliona celata* is the dominant species in inshore waters along our coast. It is apparently capable of occupying a larger proportion of the calcareous substratum necessary for its early life than the other species (chiefly *C. vastifica, C. truitti,* and *C. lobata*) living sympatrically with it. On offshore scallop grounds, however, *Cliona vastifica* is the exclusive or at least the dominant boring sponge. Its incidence of occurrence on living scallop shells is much lower than the total infection of oyster shells by boring sponges. Between 75 and 80 per cent of all oysters in the New Haven region of Long Island Sound contain boring sponges;

TABLE 46

NUMBER OF LIVING OYSTERS INFECTED BY BORING SPONGES IN LONG ISLAND SOUND

SPECIES OF SPONGE INFECTING OYSTERS	NUMBER OF OYSTERS INFECTED	PERCENTAGE OF TOTAL
Cliona celata	81	40.5
Cliona vastifica	46	23.0
Cliona celata and *Cliona vastifica*	14	7.0
Cliona lobata	7	3.5
Cliona celata (Dead colonies)	10	5.0
Sponge colonies absent	42	21.0
TOTAL	200	100.0

TABLE 47

NUMBER OF SHELLS OF DEAD OYSTERS INFECTED BY BORING SPONGES IN LONG ISLAND SOUND

SPECIES OF SPONGE INFECTING SHELLS	NUMBER OF SHELLS INFECTED
Living *Cliona celata* colonies	14
Dead *C. celata* colonies*	19
Total number of *C. celata* colonies	33
Living *C. vastifica* colonies	5
Dead *C. vastifica* colonies*	16
Total number of *C. vastifica* colonies	21
Shells with both species, *C. celata* and *C. vastifica*	7
Cliona lobata	4
Shells lacking sponge colonies	35
TOTAL	100

* The clionid galleries in some of these shells may have been excavated by sponges while the oysters were still alive and before the shells were thrown back in the water as cultch.

whereas the incidence of infection of scallops by clionids in Massachusetts Bay and the Gulf of Maine is of the order of 25 per cent. The higher rate of infection of oysters is doubtless partly explicable in terms of the tendency of these molluscs to clump on old shells. In this way a single sponge colony can spread asexually to six or seven oysters.

It is probable that the faster growth rate of *C. celata,* which is manifest in its eventual overgrowth of the shells it infects to form a free-living colony, explains the greater abundance of this form over all other species in certain regions. *Cliona vastifica* grows more slowly; seldom, if ever, forms free-living colonies; and seems to be incapable of fully exploiting the ecological niche which is available to it on the scallop beds. The absence of *C. celata* from the Massachusetts Bay scallop beds may result from an incapacity to produce larvae in the cooler offshore waters with a consequent dependence upon inshore stocks to colonize deeper areas. Since oyster beds north of Cape Cod are largely depleted, the boring sponge cannot attain the abundance which it does south of the Cape, and the likelihood of its establishment in offshore waters from inshore-produced larvae is slight. Its absence from the northern part of the Gulf of Maine and from the Bay of Fundy is consistent with its range in inshore waters in the North Atlantic. Its northernmost recorded occurrence in North America is in Malpeaque Bay, Prince Edward Isl.; it is absent from Greenland (Brøndsted, 1914, 1916, 1933a, 1933b). In the eastern North Atlantic it occurs at the Shetland Isls. (Bowerbank, 1882) and in Stavanger Bay, Norway (Burton, 1930a); it is absent from northern Norway (Burton, 1930a), the Faroes (Brøndsted, 1932), and the White Sea (Merejkowsky, 1879; Swartschewsky, 1906). This distribution suggests that the temperature for larval production is the limiting factor in its northern distribution since it is perennial in growth along the Atlantic Coast of the United States where winter temperatures equal those of Arctic regions. Vertically, its distribution extends down to 200 meters and, to the present writer's knowledge, its occurrence in deep waters is restricted to tropical areas except for one record at 130 meters off the west coast of France where the mean annual temperature is about 15° C.

The occurrence of *Cliona celata* and *Cliona vastifica* in the North and Baltic Seas is shown in figure 45. *Cliona celata* is widely distributed on the oyster beds of Holland, the East and North Frisian Islands, Denmark, and Schleswig-Holstein (Arndt, 1935, 1943). Levinsen (1893) records *C. celata* in the Skagerrak and Cattegat at depths of 18–32 meters. So far as present records indicate, *Cliona vastifica* is largely absent from this extensive region. One specimen has been reported from the deepest part of the Kieler Bucht (Arndt, 1933), and there are several records of its occurrence on the *Lophohelia* banks off the Gullmars and Väderö Fjords and in the Koster area, all in southwestern Sweden (Fristedt, 1885; Alander, 1942). Arndt (1943) records it from Øresund and from the North Sea north of the 60 meter line. The Swedish records are from depths of 40 meters or over. (Such depths occur very close to shore in this region contrary to the case along the Danish coast which slopes gradually.) *Cliona celata* is reported by Fristedt and Alander as being common in the shallow coastal waters of Sweden. Alander has suggested that the restriction of *C. vastifica* to deep waters in the Swedish area may be a result of its incapacity to withstand the low salinities of the surface waters; however, the salinities in this region vary from 30 to 20 o/oo (Välikangas, 1933) and it is unlikely that such would prove lethal to this species. Bottom salinities in the Kieler Bucht vary from 20 to 15 o/oo (Schulz, 1932).

Nasonov (1925) has reported *Cliona vastifica* from the Barents Sea along the

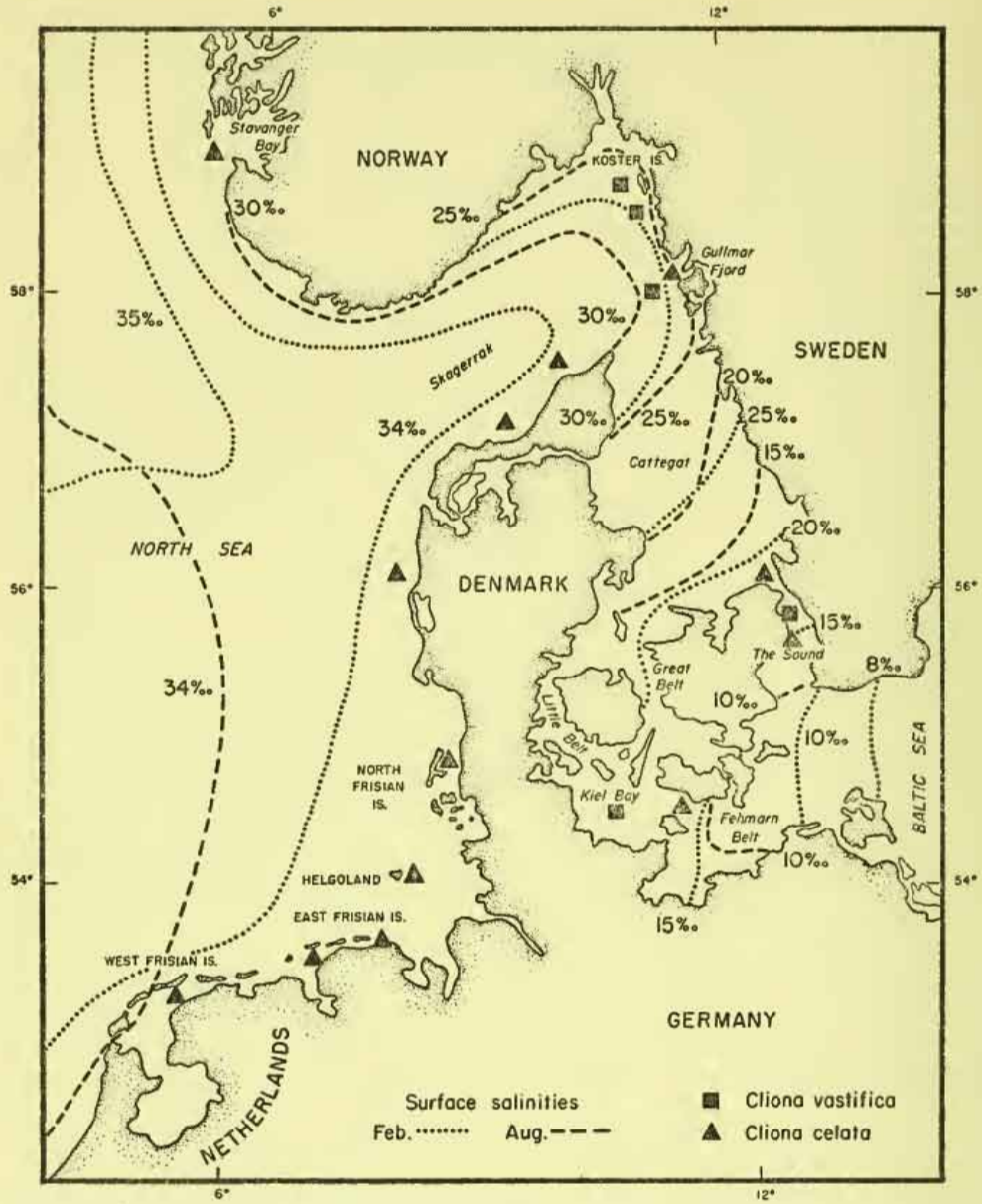


FIGURE 45. Distribution of clionids in the North Sea area in relation to salinity.

northern shore of the Kola Peninsula. It was found at a depth of 140 meters in the Kola Gulf near the eastern shore of Sedlovaty Island and in shallow water in the Bay of Oura of the Motovka Gulf.

DISTRIBUTION IN THE MEDITERRANEAN REGION: The Adriatic Sea is especially well known as a result of the work of Lendenfeld (1898) and Volz (1939). The latter author in particular has made very careful studies of the ecological relationships of the nine species of the family Clionidae in the region of Rovigno d'Istria. His observations are summarized in figure 46; see also Hartman (1957).

Volz reports the greatest abundance of clionids in the littoral terrace extending from low water springs to a depth of 25 meters. Here seven species coexist with *Cliona celata* and *C. vastifica,* which are abundant only in shallow water and again in deep water. Throughout most of the terrace these two species tend to occur chiefly in mollusc shells and assume an insignificant role compared to *C. viridis* and *C. vermifera* and other dwellers in limestone.

In the deeper waters below the limestone terrace is an area of sand and shells which supports three species of boring sponges; *Cliona vastifica, Cliona viridis,* and *Cliona celata,* in order of abundance. *C. vastifica* occurs almost exclusively in mollusc shells, especially those of mussels. *C. viridis,* on the other hand, occurs mainly in association with coralline algae. *Cliona celata* is a less common inhabitant of both substrata.

In addition, *Cliona vastifica* lives in the narrow zone between low tide neaps and low tide springs, and is the only species to inhabit the limestone cliff at this level. Thus, in summary, it may be said that *C. vastifica* is the most widespread

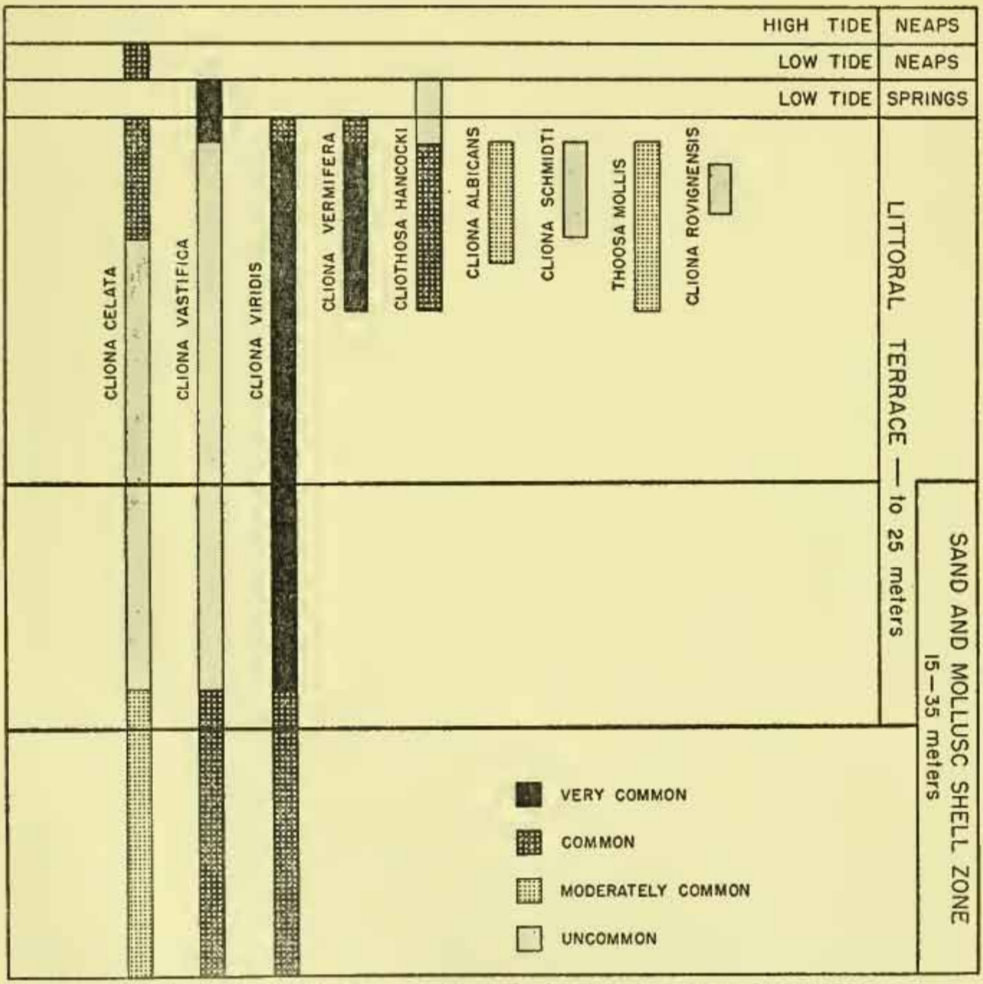


FIGURE 46. Vertical distribution of clionids at Rovigno. Data after Volz.

species in the Rovigno district, occurring from low water neaps down to the deep offshore waters. In the two extreme environments it is the dominant species; in the intermediate littoral terrace it is pushed into an insignificant place by competition with the fast-growing *C. viridis* and *C. vermifera*. *C. celata* is a minor species in this part of the Adriatic, although it ranges throughout the littoral terrace and into the sand and shell zone, and also is able to survive in tidal pools above mean low water when it is thrown up into such locations by the action of the surf. It does not occur on the oyster beds in the canal of Leme where the salinity is reduced, although *C. vastifica, C. viridis,* and *C. vermifera* are found there in limited numbers.

Several other Mediterranean records of *C. celata* and *C. vastifica* are of interest in the present connection. Seurat (1934) noted that *C. vastifica* alone occurs in the zone between low water neaps and low water springs in the Gulf of Gabès, thus extending the observations of Volz. Both species occur in the Étang de Thau, a brackish water inlet on the south coast of France (Topsent, 1925b).

The most frequently recorded boring sponge in the Black Sea was described by Nasonov (1883) as a new species, *Cliona stationis*. It has been reported from the Bay of Sevastopol (Nasonov, 1883, 1924; Swartschewsky, 1905; Kudelin, 1910), from the Bay of Odessa (Kudelin, 1910), and from Sukhumi (Nikitin, 1934). According to Nasonov's figures (1883) the spicules are highly variable in form. Many of the tylostyles are characterized by irregular knobs and swellings along their lengths, and the oxeas, which are usually spined but may be smooth, show a tendency toward centrotylosis. The spirasters are rodlike to contorted in shape, and some have central swellings. Swartschewsky (1905) figured quite normal tylostyles and acanthoxeas, the latter without central swellings, and has synonymized *C. stationis* with *C. vastifica*. Kudelin (1910) also reports this sponge as *C. vastifica*. Nikitin (1934) retains the name *C. stationis*. It is apparent that the *vastifica*-like clionids of the Black Sea are highly variable in spiculation and are probably best regarded as a subspecies, *Cliona vastifica stationis* (Nasonov). Czerniavsky's (1880) species, *C. pontica,* is of uncertain status, as mentioned earlier, but it is possible that it represents an extreme variant of *vastifica*.

FURTHER DISTRIBUTION: Annandale (1915a) states that *Cliona vastifica* is the commonest species in the littoral zone of the east coast of India. It often makes its way into brackish waters in this region, occurring in Chilka Lake at Orissa and the Ganjam district (in shells of *Ostrea* and *Purpura*), in the Adyar River at Madras, and in the Ennur Backwater (in *Ostrea* shells). It is common in the Persian Gulf in shells of *Avicula* and *Margaritifera;* it occurs in *Placuna* shells from Palk Straits (5½ fathoms) and in the shells of *Oliva* and *Malleus* from the Andaman Islands. *Cliona celata* is not nearly as common in Indian waters, only three records being given by Annandale. These are from a station 28 fathoms in depth off the coast of Burma (in calcareous algae); from shallow water at Madras (in *Pyrula*); and from 6½ fathoms in the Gulf of Manaar (also in *Pyrula*).

In Chilka Lake, *Cliona vastifica* is very abundant on the oyster beds of the outer channel (Annandale, 1915b). The salinity of this part of the lake is about as high as that of the open sea (*ca.* 35 o/oo) during eight months of the year, but in December flood waters reduce the salinity to values between 17.4 and 5.3 o/oo. A condition of almost fresh water is maintained for the next three months. Living specimens of *Cliona vastifica* have been taken from Chilka Lake when the salinities were 8.9 and 14.1 o/oo. The change back to normal sea water often

occurs in the course of a single day. Although *C. vastifica* is most abundant in the *Ostrea* shells of the outer channel, it also occurs in the main area of the lake where the salinity is always reduced; in this area it inhabits the shells of *Purpura* (*Thais*) *carinifera.*

SUMMARY OF THE ZOOGEOGRAPHY OF THE CLIONIDAE: Let us examine the zoogeographical data in an attempt to determine some of the factors which have led to speciation in the family Clionidae. In the first place, the Mediterranean data tend to confirm the generally held idea that the center of speciation of this family of sponges is in the warm waters where calcareous matter abounds. Here in shallow waters nine species of clionids coexist. Coral reefs have been considered as the most probable sites of origin of boring sponges, and in this regard it might be mentioned that the spirastrellids which grow in cavities in corals are suggestive of early stages in the development of the excavating habit. Both Vosmaer (1911) and Burton (1934) have noted species of the genus *Spirastrella* which are restricted in occurrence to cavities in corals. It is uncertain whether or not the sponge colony has helped in forming the cavities; certainly they are not nearly as complex as the galleries actively excavated by clionids. But the obligatory relationship of some spirastrellids with this type of habitat suggests a stage in the development of the boring process. Morphologically, *Spirastrella* is closely allied to *Cliona;* indeed, the most diagnostic character separating them is the boring habit of the latter.

Extension of range into temperate regions has depended upon an abundance of mollusc shells such as occur in coastal regions where *Ostrea* abounds or in offshore areas where *Pecten* lives.

If the discussion is restricted now to *Cliona celata* and *Cliona vastifica,* it is found that the overall ranges are practically coextensive, but that local occurrences are variable in the well-studied areas which have been cited as examples. *C. celata* is the dominant form on the oyster beds of the American Atlantic Coast and in the North Sea and Belt seas of Western Europe. In the first locality *Cliona vastifica* occurs sympatrically with *C. celata* at least as far north as Long Island Sound, but is only about half as abundant as the first-named species. On western European oyster beds (at least those in the North Sea) *Cliona celata* is the only species found. On both sides of the Atlantic in temperate regions, the range of *C. vastifica* extends into deeper offshore waters: the scallop areas of Massachusetts Bay and the Gulf of Maine; the *Lophohelia* banks off southwestern Sweden; the southern part of the Barents Sea; and the deepest parts of the Kieler Bucht. In these areas it is without competition from other clionids for substratum. Where oysters are especially common both species can find sufficient substratum to coexist; under such conditions *C. celata* predominates in temperate waters. Where oysters are less common (as in the inshore waters of the Gulf of Maine) present evidence indicates that *Cliona celata* is the sole inhabitant of these shells, and *C. vastifica* has exploited offshore areas.

In the warmer regions of the world, *Cliona vastifica* is more common than *C. celata.* In the Adriatic, e.g., *C. vastifica* occurs from the low water neap tide level down to the deep sand and shell areas. It is the sole clionid in the restricted area between low water neaps and low water springs; but it fares only moderately well in the multispecific competition for substratum which occurs in the littoral terrace. Here two other species (*Cliona viridis* and *Cliona vermifera*) are dominant and six other species occur in the same area. At least two of these occupy strictly delimited niches. *Cliona vastifica* tends to prefer mollusc shells although it is also found in the limestone cliff; *Cliona celata* is common in the littoral terrace in

shells and in limestone. Finally in the deeper areas, *C. vastifica* assumes the dominant role again, inhabiting the mollusc shells which are abundant there. *C. viridis* is less common and occurs chiefly in coralline algae; *C. celata* is of uncommon occurrence in both shells and algae.

Along the coasts of India, *Cliona vastifica* is again the abundant form with *C. celata* of less common occurrence.

Cliona vastifica is, in the final analysis, a more adaptive and plastic species, being capable of inhabiting a wider variety of habitats in regard to depth, reduced salinity, and exposure to air than is true of *C. celata*. A factor of importance in the wider tolerances of *C. vastifica* is doubtless the capacity to form gemmules in which state it can live through periods of stress. *Cliona celata* is better adapted to exploit such habitats as the oyster beds of temperate regions by virtue of its faster growth rate, larger size, and probable concomitant reproductive advantages. However, along with its specializations which enable it to exploit a particular habitat, is a restricted adaptability to environmental extremes. Thus, it does not occur on the scallop beds, possibly because it cannot reproduce at the low temperatures present at such depths.

In the warm waters of the Adriatic the dominating position of *C. celata* disappears before that of two other species which seem better adapted to existence in limestone. Still stranger is the fact that in Indian waters *C. vastifica* is dominant over *C. celata* on oyster beds. These facts suggest that *C. vastifica* is the older species and that *C. celata* arose in temperate regions where it is well adapted to exploit the beds of gregarious molluscs occurring there. It has since spread into warmer seas, but always occupies a minor role in the competition for substratum in these localities. Even on the Indian oyster beds it does not assume the dominant position which it occupies under similar circumstances in temperate waters. Young specimens of *C. celata* (in Europe at least) often possess oxeas and spirasters, suggesting an origin from a species like *C. vastifica* with a full complement of spicules. The fact that young specimens of *C. celata* with microscleres have seldom been recorded from American waters suggests that this species developed in the Old World and subsequently spread to the American continent.

A NOTE ON THE CONTROL OF BORING SPONGES

Since the clionids infect such a high percentage of the oysters in Long Island Sound and other inlets along the North American Coast, and since their excavations make the shells of oysters weak so as to hinder processing in canning factories, it is of considerable interest to oystermen in these areas to develop control measures. Topsent (1900) suggested that immersion for a short time in fresh water would suffice to kill the boring sponges in oysters. De Laubenfels (1947) dipped an infected oyster "briefly" in fresh water and noted that the boring sponge colony failed to recover in sea water. The present experiments indicate that at temperatures near 23° C. a period of exposure to fresh water between one and two hours would be necessary to kill the sponge colonies. Even then it is quite probable that restitution bodies would arise from the cells which were hidden in the recesses of the excavations and eventually regeneration would ensue. In experiment 1A of the present investigations it was found that although recovery from one hour of exposure to fresh water was slow, after a period of 17 days in sea water, the sponges were fully functional once again. Under the conditions of oyster farming practiced in America, exposure of the animals to fresh water for several hours is hardly feasible. If a substance toxic to the sponge colonies were found it is con-

ceivable that it could be effectively applied in solution to piles of oysters on the decks of boats.

Another approach to the problem concerns the type of cultch used. Normally dead oyster and clam shells are planted out on the beds to serve as substrata for the attachment of spat. This cultch is planted out in late spring in time for the most intensive setting period of oysters in July. The setting period of boring sponges is in August and September so that this calcareous cultch is subject to infection the same year in which it is planted out. Since a single shell often supports six to eight young oysters, it is obvious that during the following year of growth the sponges can infect all of these animals by asexual spreading. It is likely that the high incidence of infection among oysters as compared to scallops is a result of this very fact. Hence it is suggested here that a non-calcareous cultch such as broken bricks or tiles would decrease the incidence of clionid infection by isolating more of the oysters from their neighbors and thus preventing asexual spreading of the colonies. Perhaps coating the cultch shells with black varnish would protect them from infection by boring sponges; this method was suggested by Orton (1937) as a means of darkening shells to attract more spat.

Additional information is needed concerning the intensity of settling of clionid larvae. The work reported here from Milford Harbor indicated a rather low rate of infection by this means; however, conditions may be quite different on the oyster beds at New Haven Harbor where clionids reach a peak of abundance.

SUMMARY

1. Both *Cliona celata* and *C. vastifica* are capable of functioning normally in salinities lower (20 o/oo) than they are likely to meet in offshore waters in Long Island Sound.

2. Both species can recover to normal activity after brief exposures to salinities down to 10 o/oo (or lower).

3. Tolerance of clionids to low salinities is inversely related to temperature.

4. *Cliona vastifica* is more tolerant of exposure to low salinities than *C. celata*.

5. Populations of *Cliona vastifica* have invaded brackish water in a number of regions of the world and have undergone parallel morphological changes in each area, although the extent of differentiation varies. Three populations along the American Atlantic Coast apparently merit specific rank.

6. The zoogeography of the family Clionidae is discussed. It is found that *Cliona celata* is the dominant species on oyster beds in temperate regions; *Cliona vastifica* dominates on Indian oyster beds. In each case the other species assumes a secondary position in the same area and in some cases occurs as the dominant form in adjacent offshore areas.

7. *Cliona celata* probably originated in the Old World in temperate regions and has since spread to tropical areas where it has difficulty in invading niches already filled. The generally increased size and higher growth rate of *Cliona celata* together with higher reproductive capacity have favored its establishment in inshore temperate regions, but in warmer areas other unknown factors operate in keeping it in a secondary position.

8. It is suggested that the use of a non-calcareous cultch for collecting oyster spat would reduce the incidence of infection of oysters by boring sponges.

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SYSTEMATIC INDEX

Numbers in italics indicate page on which subject is illustrated; plate references are in CAPITAL Roman numerals.

SUBJECT INDEX

Numbers in italics indicate page on which subject is illustrated; plate references are in CAPITAL Roman numerals.

PLATE 1

Fig. 1. *Cliona celata*. Living colony, α-stage, growing in shell of *Crassostrea virginica*. New Haven Harbor; 7 meters. Photographed in running sea water in laboratory. x 7/10.

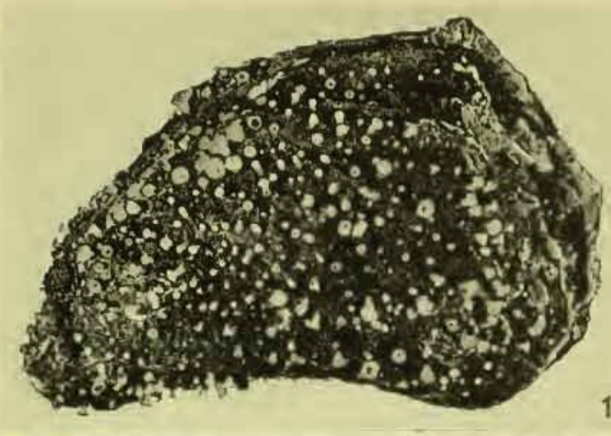
Fig. 2. Portion of same colony showing incurrent papillae and oscule. x 2.8.

Fig. 3. *Cliona celata*. β-stage, overgrowing shell of *Crassostrea virginica*. New Haven Harbor; 7 meters. x 3/4.

Fig. 4. *Cliona celata*. γ-stage, photographed soon after removal from water. New Haven Harbor, 9 meters. x 1/4.

Fig. 5. *Suberites ficus*. Block Island Sound; 40 meters. YPM #795 (dried specimen). x 1/3.

Fig. 6. Cultch bag used in studies of sponge settling. x 1/8.



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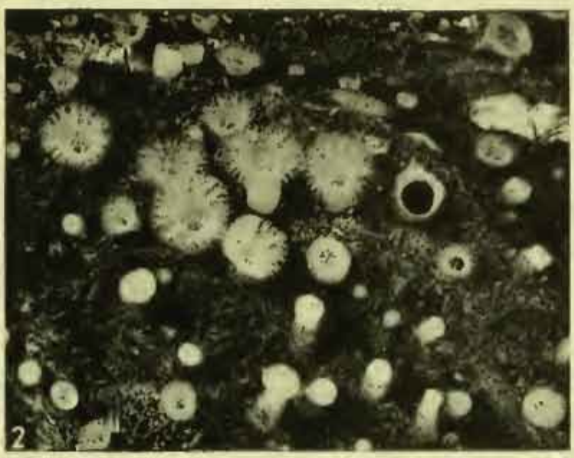

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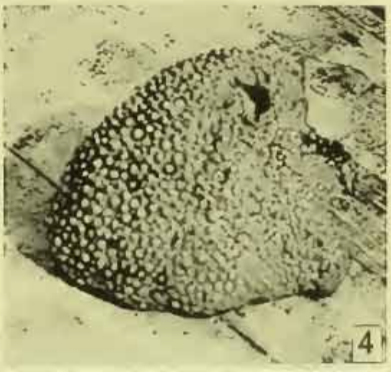

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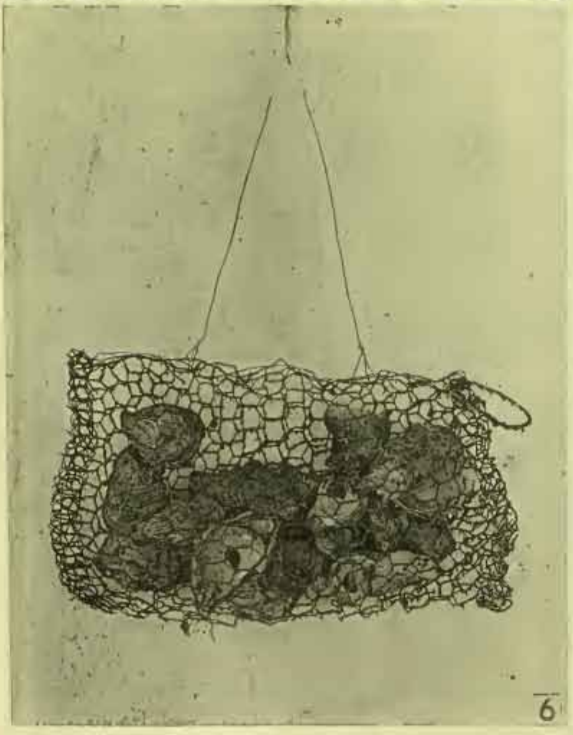

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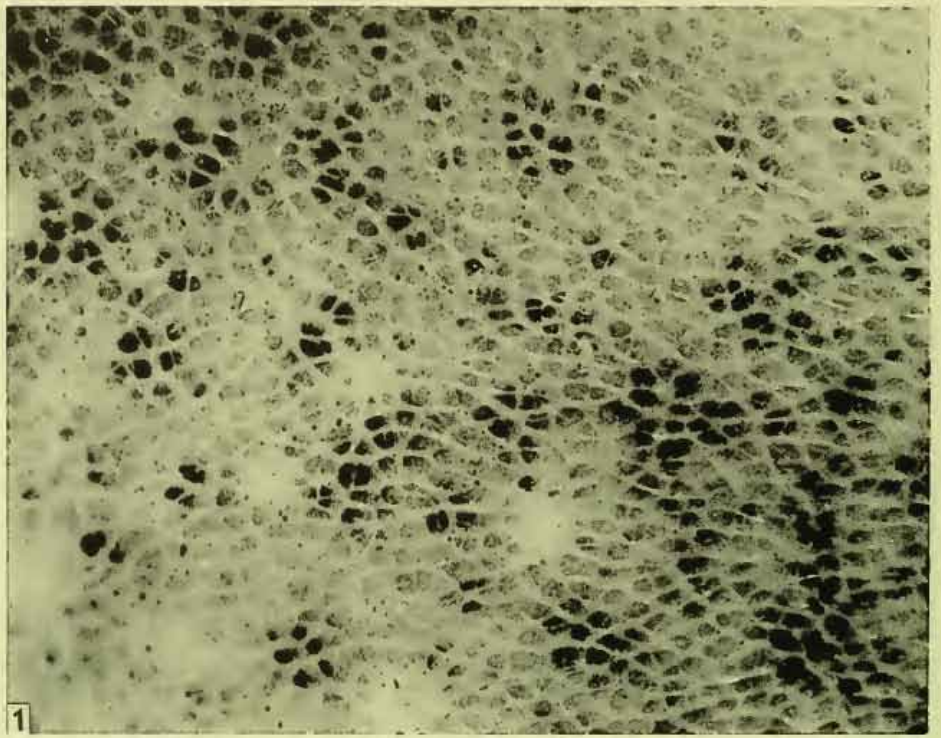

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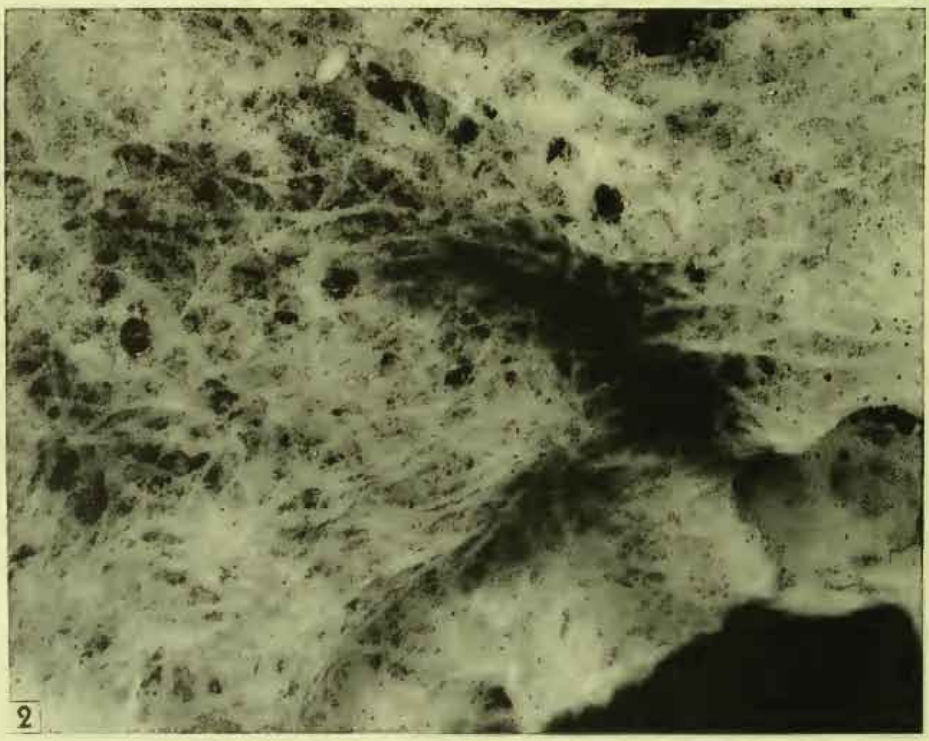

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PLATE 2

Fig. 1. *Halichondria panicea*. Pattern of dermal skeletal tracts. Plymouth, England, YPM #2097. x 24.

Fig. 2. *Halichondria bowerbanki*. Pattern of dermal skeletal tracts. Double Beach (Branford), Conn. YPM #2019E. x 21.

PLATE 3

Variations of colony form in *Halichondria bowerbanki*
(All photographs from specimens preserved in alcohol.)

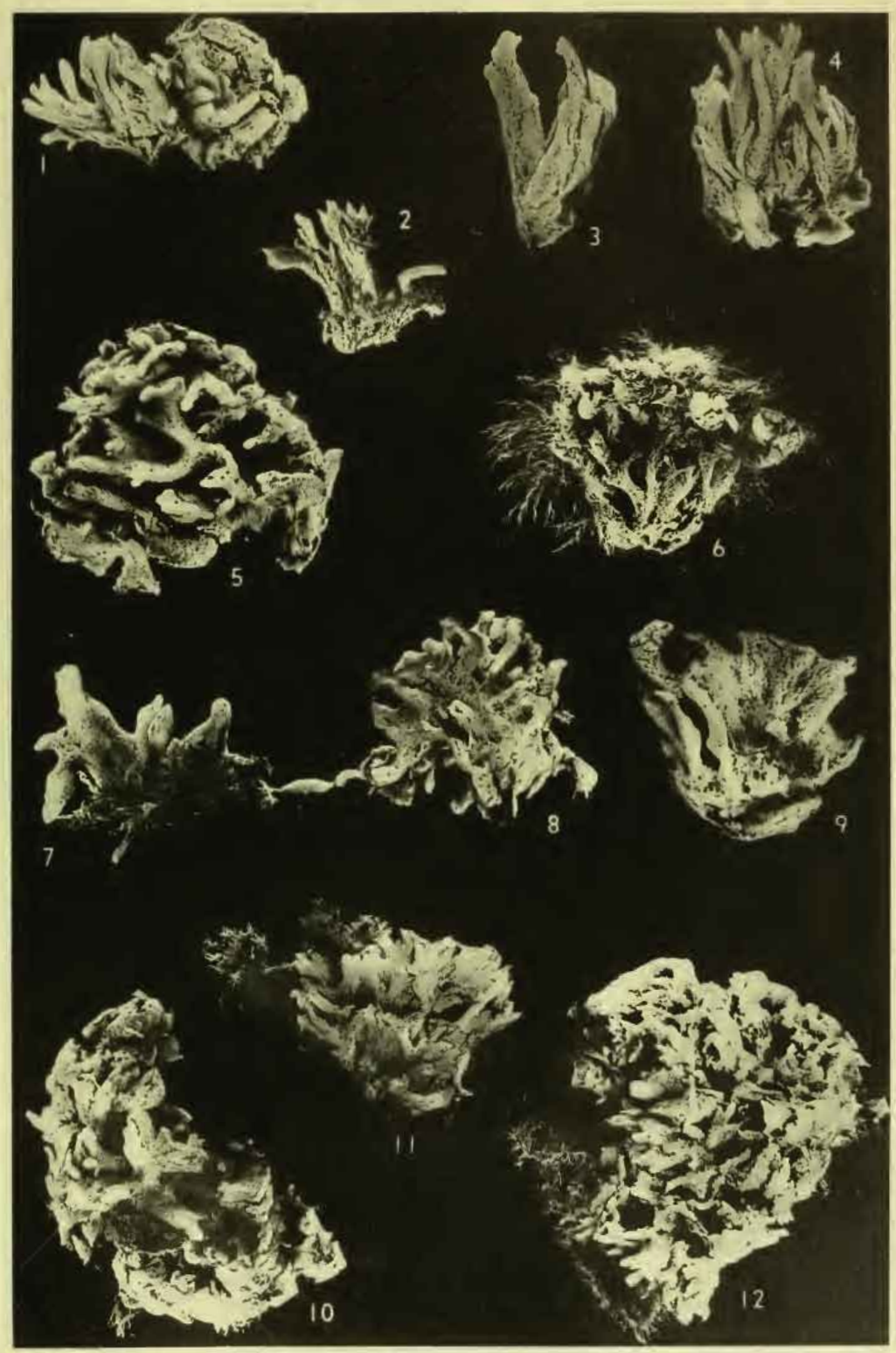
Figs. 1, 2, 3. Colonies with massive base and both rounded and lamellate vertical branches; viewed from the side. Figs. 1, 2: Lagoon Pond, Martha's Vineyard, YPM #940. x 1/2. Fig. 3: Double Beach (Branford), Conn. YPM #2019D. x 1/2.

Fig. 4. Colony with massive base and rounded, anastomosing branches; viewed from side. Hammonasset, Conn. YPM #2024D. x 1/2.

Fig. 5. Colony with massive base and anastomosing, rounded branches; viewed from above. Hammonasset, Conn. YPM #2024E. x 1/2.

Figs. 7, 8. Colonies with vertical processes which do not anastomose. Double Beach (Branford), Conn. YPM #2019E. x 1/2.

Figs. 6, 9-12. Colonies with massive base and lamellate processes. Fig. 6: Lagoon Pond, Martha's Vineyard. YPM #940. x 1/2. (Viewed from side.) Fig. 9: Double Beach (Branford), Conn. YPM #2019E. x 1/2. (Viewed from side.) Figs. 10, 11, 12: Bradley Point, West Haven, Conn. YPM #2026B. x 1/2. (Viewed from above.)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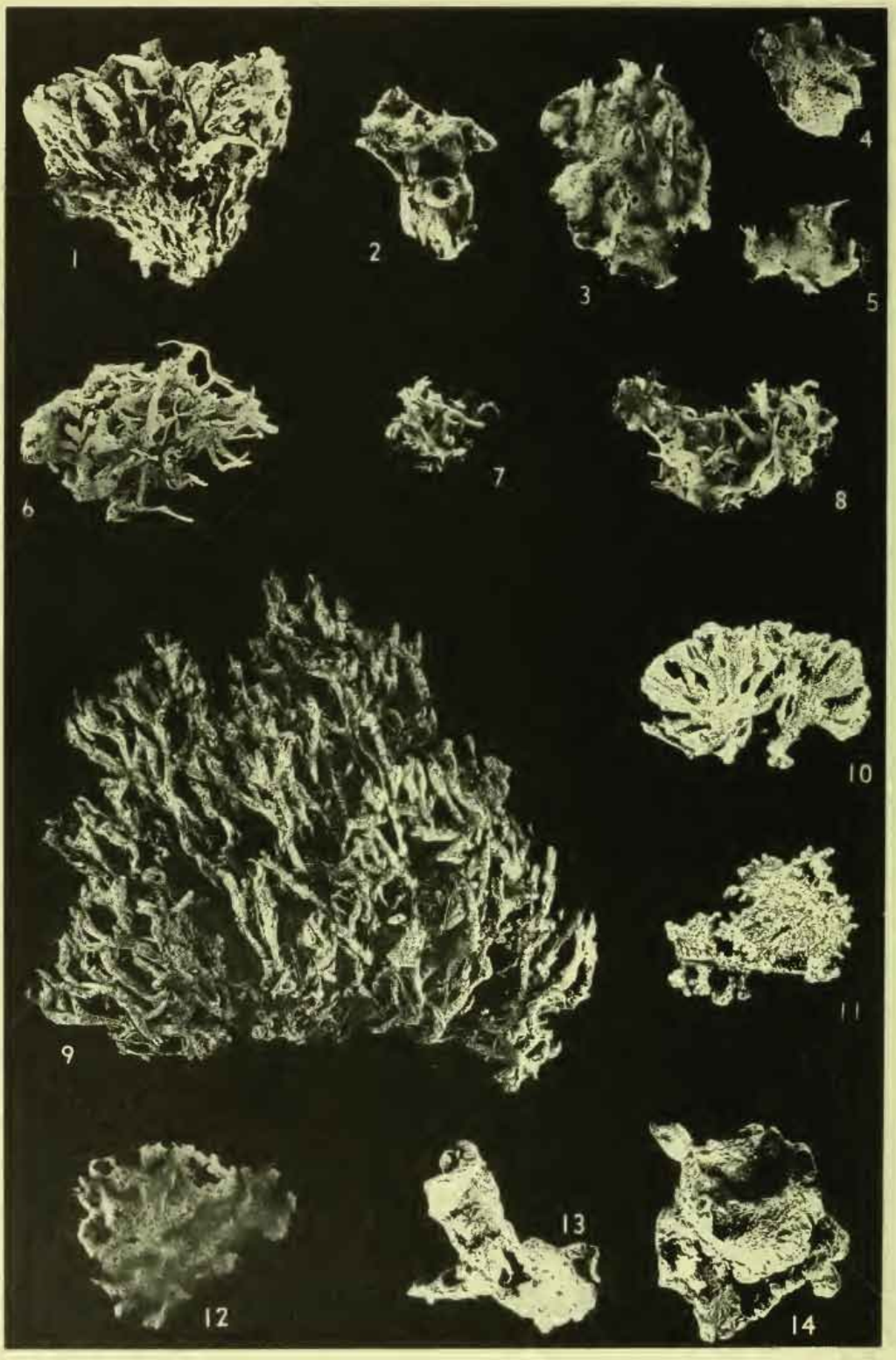
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PLATE 4

Variations of colony form in *Halichondria bowerbanki*
(All photographs from specimens preserved in alcohol.)

Fig. 1. Colony consisting of a mass of anastomosing, rounded branches; viewed from side. Off Lighthouse Pt., New Haven, Conn. YPM #814. x 1/2.

Fig. 2. Colony with chimney-like process; viewed from above. Off Lighthouse Pt., New Haven, Conn. YPM #814. x 1/2.

Fig. 3. Encrusting colony with vertical processes; viewed from above. Double Beach (Branford), Conn. YPM #1893D. x 7/10.

Figs. 4, 5. Thin, encrusting colonies without processes; viewed from above. Double Beach (Branford), Conn. YPM #1893D. x 7/10.

Figs. 6, 7, 8. Colonies with thin, anastomosing branches; viewed from above. Fig. 6: Double Beach (Branford), Conn. YPM #840. x $>$ 1/2. Figs. 7, 8: Double Beach (Branford), Conn. YPM #1911E. x $>$ 1/2.

Variations of colony form in *Microciona prolifera*.
(All photographs from dried specimens.)

Fig. 9. Large colony consisting of an anastomosis of branches; viewed from side. Off Lighthouse Pt., New Haven, Conn. YPM #815. x 2/5.

Fig. 10. Colony with palmate branching habit; viewed from side. Off Mansfield Pt. (East Haven), Conn. YPM #808. x 1/2.

Fig. 11. Encrusting colony with short vertical branches; viewed from above. Off Mansfield Pt. (East Haven), Conn. YPM #808. x 1/2.

Lissodendoryx and *Microciona*

Fig. 12. *Lissodendoryx isodictyalis*. Double Beach (Branford), Conn. YPM #2096. x $<$3/5. (Alcohol)

Fig. 13. *Microciona prolifera*. Lamellate colony. New Haven, Conn. YPM #262. x 1/2. (Dried specimen)

Fig. 14. *Microciona prolifera*. Cup-shaped colony. New Haven, Conn. YPM #262. x 1/2. (Dried specimen)

PLATE 5

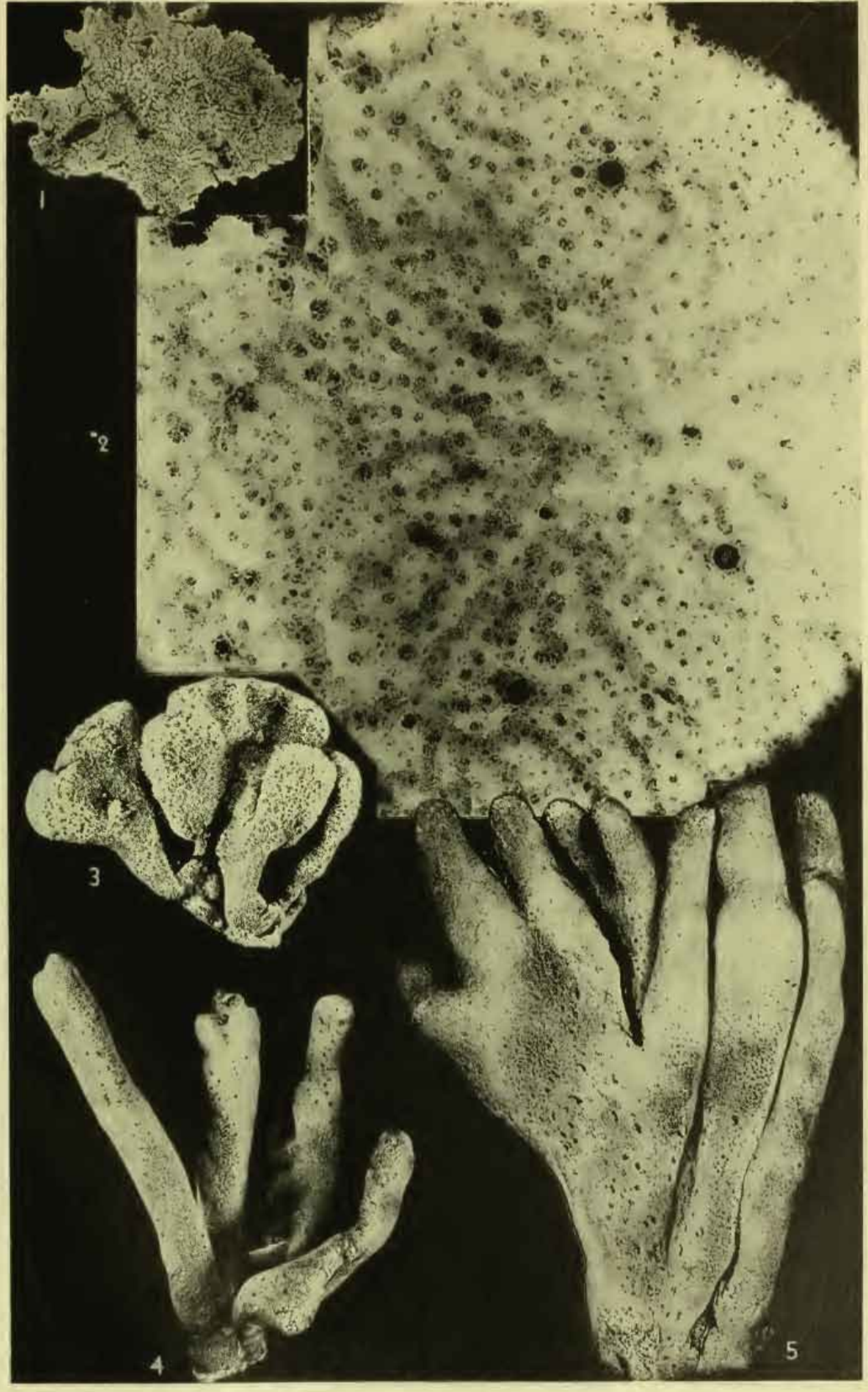
Fig. 1. *Haliclona canaliculata*. Colony viewed from above. Double Beach (Branford), Conn. YPM #2017. x 2/3. (Alcohol)

Fig. 2. *Haliclona canaliculata*. Upper surface of a colony showing the characteristic pattern of subdermal channels and openings from these into the interior of the sponge. Dermal pores not visible. Double Beach (Branford), Conn. YPM #1955B. x 6. (Alcohol)

Fig. 3. *Isodictya deichmannae*. Nantucket. YPM #2112. x 1/3. (Dried specimen)

Fig. 4. *Isodictya deichmannae*. Grand Banks. YPM #419. x 3/10. (Dried specimen)

Fig. 5. *Isodictya deichmannae*. Off Nantucket. YPM #2113. x < 1/2. (Dried specimen)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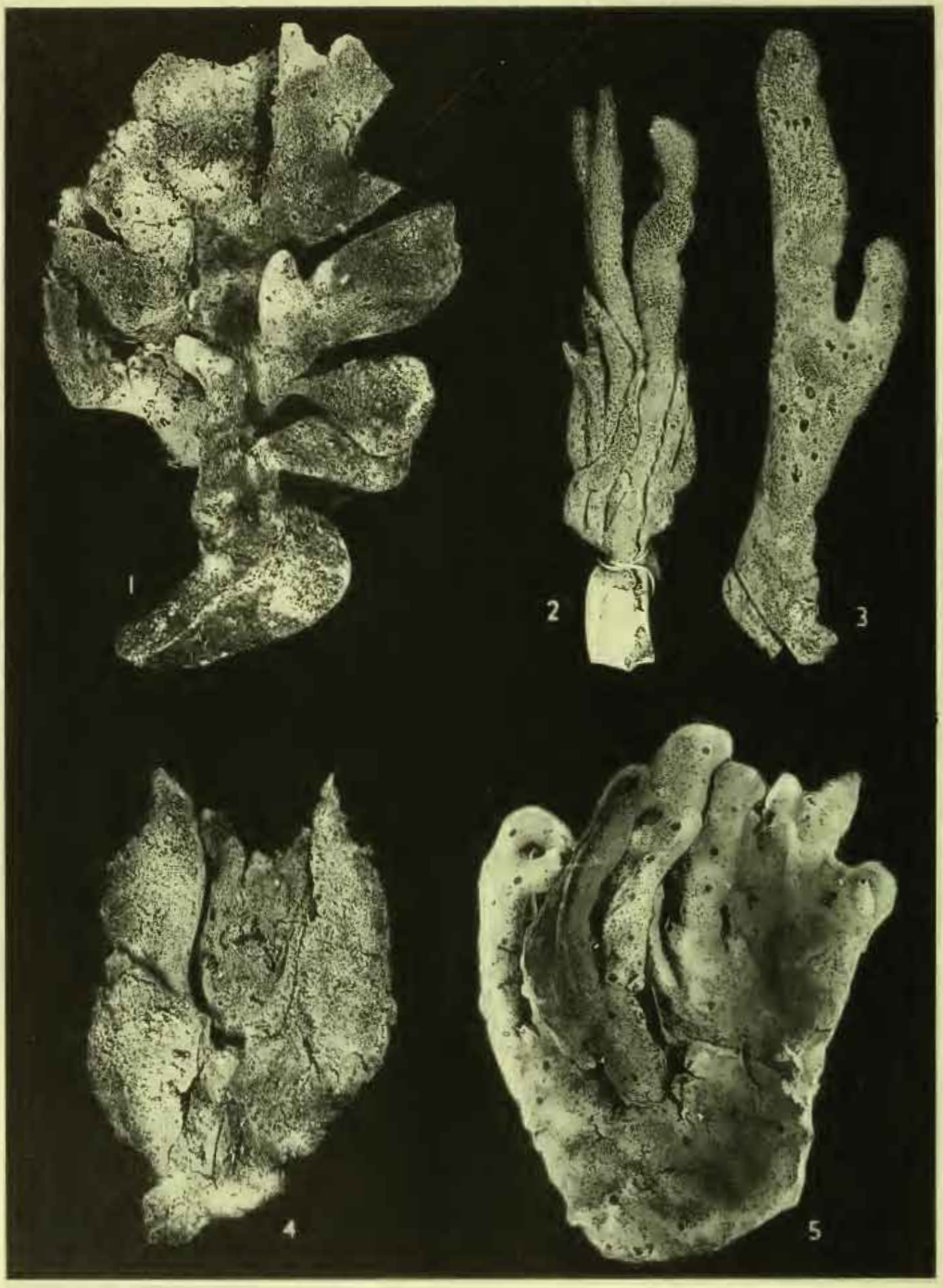
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PLATE 6

Fig. 1. *Isodictya palmata*. Kent Island, N.B. YPM #923. x 2/5. (Dried specimen)

Fig. 2. *Isodictya palmata*. Minas Basin, N.S. YPM #2114. x > 2/5. (Dried specimen)

Fig. 3. *Isodictya palmata*. Eastport, Me. YPM #151. x > 2/5. (Dried specimen)

Fig. 4. *Isodictya deichmannae*. Kent Island, N.B. YPM #890. x > 2/5. (Dried specimen)

Fig. 5. *Isodictya deichmannae*. Off New London, Conn. YPM #762. x > 2/5. (Alcohol)

PLATE 7

Fig. 1. *Haliclona oculata*. Off Sandy Point, Block Isl., R. I. YPM #783. x > 1/3. (Dried specimen)

Fig. 2. *Haliclona oculata*. Off Sandy Point, Block Isl., R. I. YPM #782. x >1/3. (Dried specimen)


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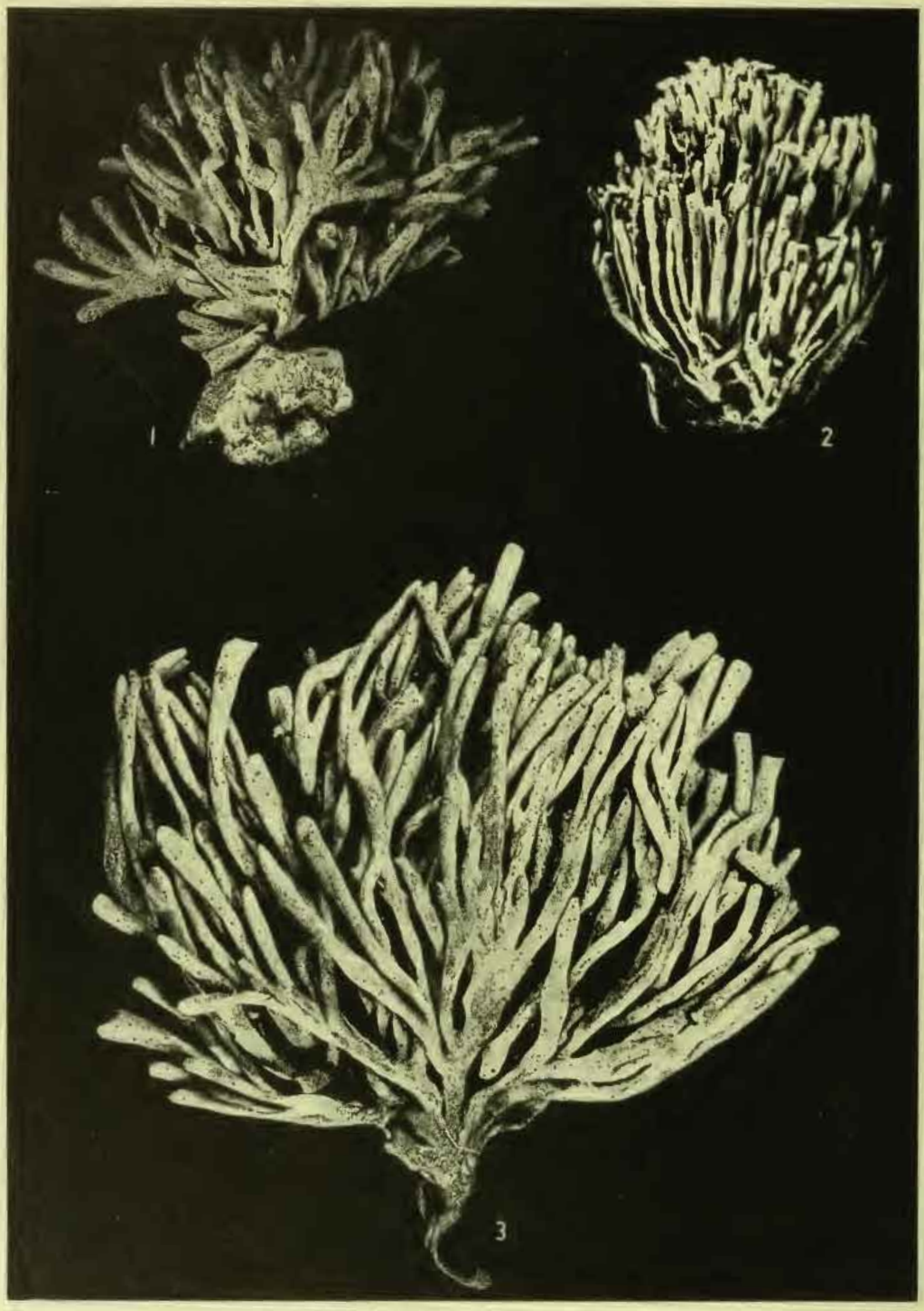
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PLATE 8

Fig. 1. *Haliclona oculata*. Off Sandy Pt., Block Isl., R. I. YPM #791. x 1/3. (Dried specimen)

Fig. 2. *Haliclona oculata*. New Haven, Conn. YPM #130. x 2/5. (Dried specimen)

Fig. 3. *Haliclona oculata*. Off Sandy Pt., Block Isl., R. I. YPM #784. x 1/3. (Dried specimen)

PLATE 9

Fig. 1. *Haliclona oculata.* Off Nantucket. YPM #2115. x < 1/3. (Dried specimens)

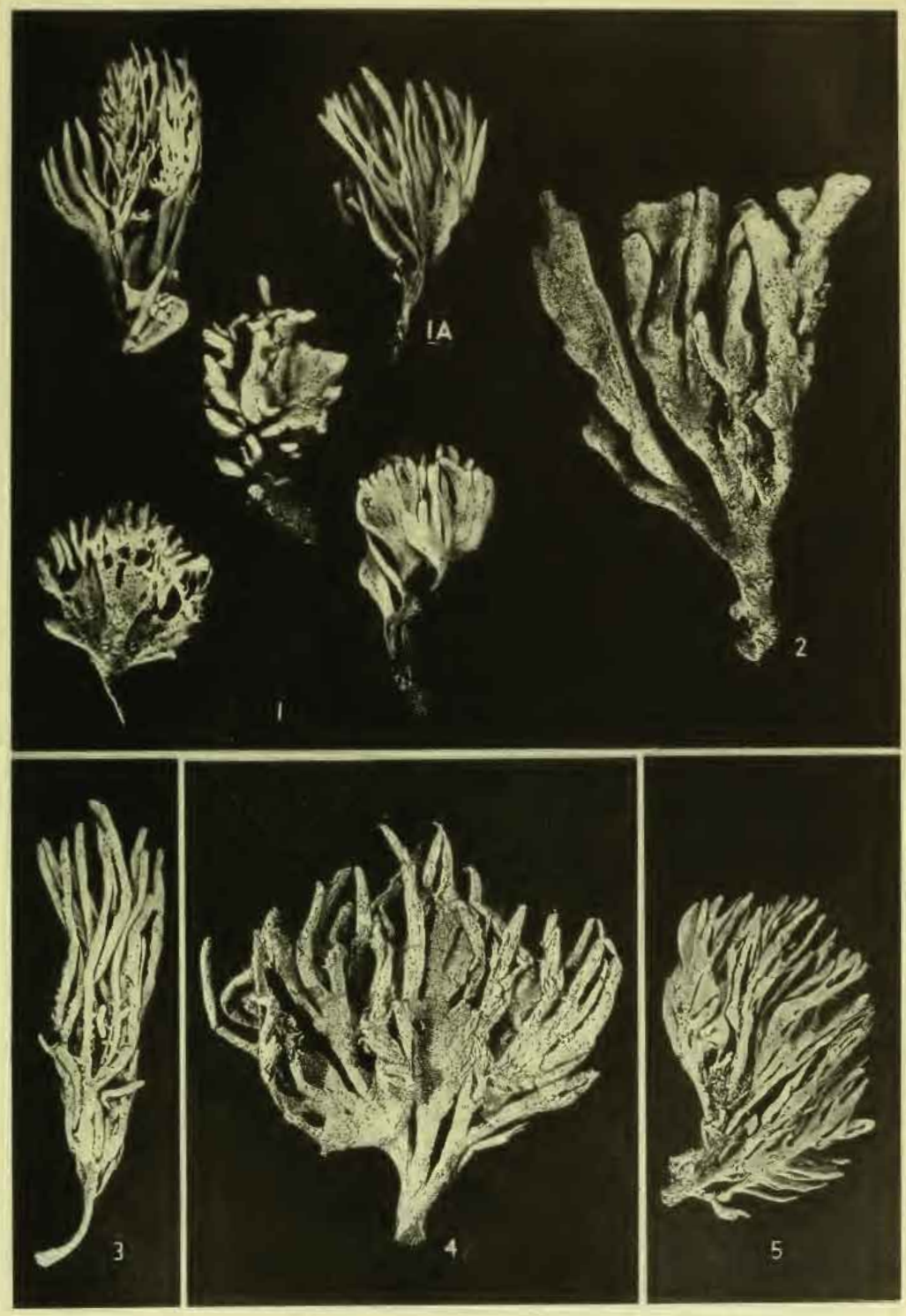
Fig. 1A. *Haliclona oculata.* Off Woods Hole, Mass. 8-20 meters. YPM #126. x <1/3. (Dried specimen)

Fig. 2. *Haliclona oculata.* Stellwagen Bank, Massachusetts Bay. 35-40 meters. YPM #965. x 1/3. (Dried specimen)

Fig. 3. *Haliclona oculata.* Off St. Valéry-en-Caux, France. YPM #1073. x 1/3. (Dried specimen)

Fig. 4. *Haliclona oculata.* Woods Hole, Mass. YPM #942. x 1/3. (Dried specimen)

Fig. 5. *Haliclona oculata.* Off Hammonasset, Conn. YPM #855. x 1/3. (Dried specimen)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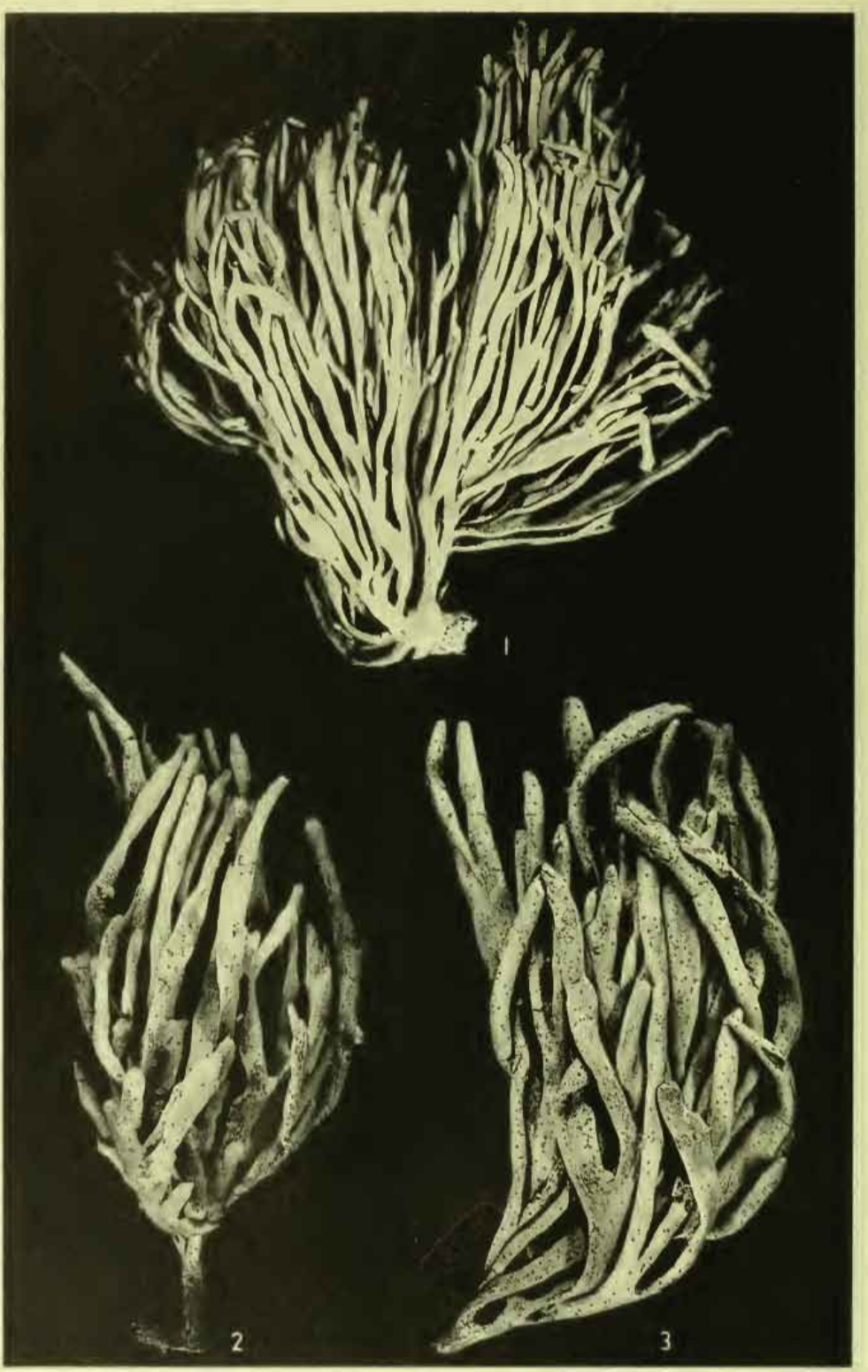
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PLATE 10

Fig. 1. *Haliclona oculata*. Portland, Me. YPM #2116. x <1/4. (Dried specimen)

Fig. 2. *Haliclona oculata*. Fipennies Ledge, Gulf of Maine; 75 meters. YPM #995. x < 1/3. (Dried specimen)

Fig. 3. *Haliclona oculata*. Stellwagen Bank, Massachusetts Bay; 35-40 meters. YPM #965. x 1/3. (Dried specimen)

PLATE 11

Variations of colony form in *Haliclona loosanoffi*.
(All photographs from specimens preserved in alcohol.)

Figs. 1, 3, 8-11. Colonies with many oscular tubules arising from an encrusting base; all viewed from above. Figs. 1, 3, 11: Milford Harbor, Conn. YPM #859. x 3/4. Figs. 8-10: Bradley Pt., West Haven, Conn. YPM #2025E. x 2/3.

Fig. 2. Colony with dichotomizing vertical branches; viewed from side. Milford Harbor, Conn. YPM#859. x 3/4.

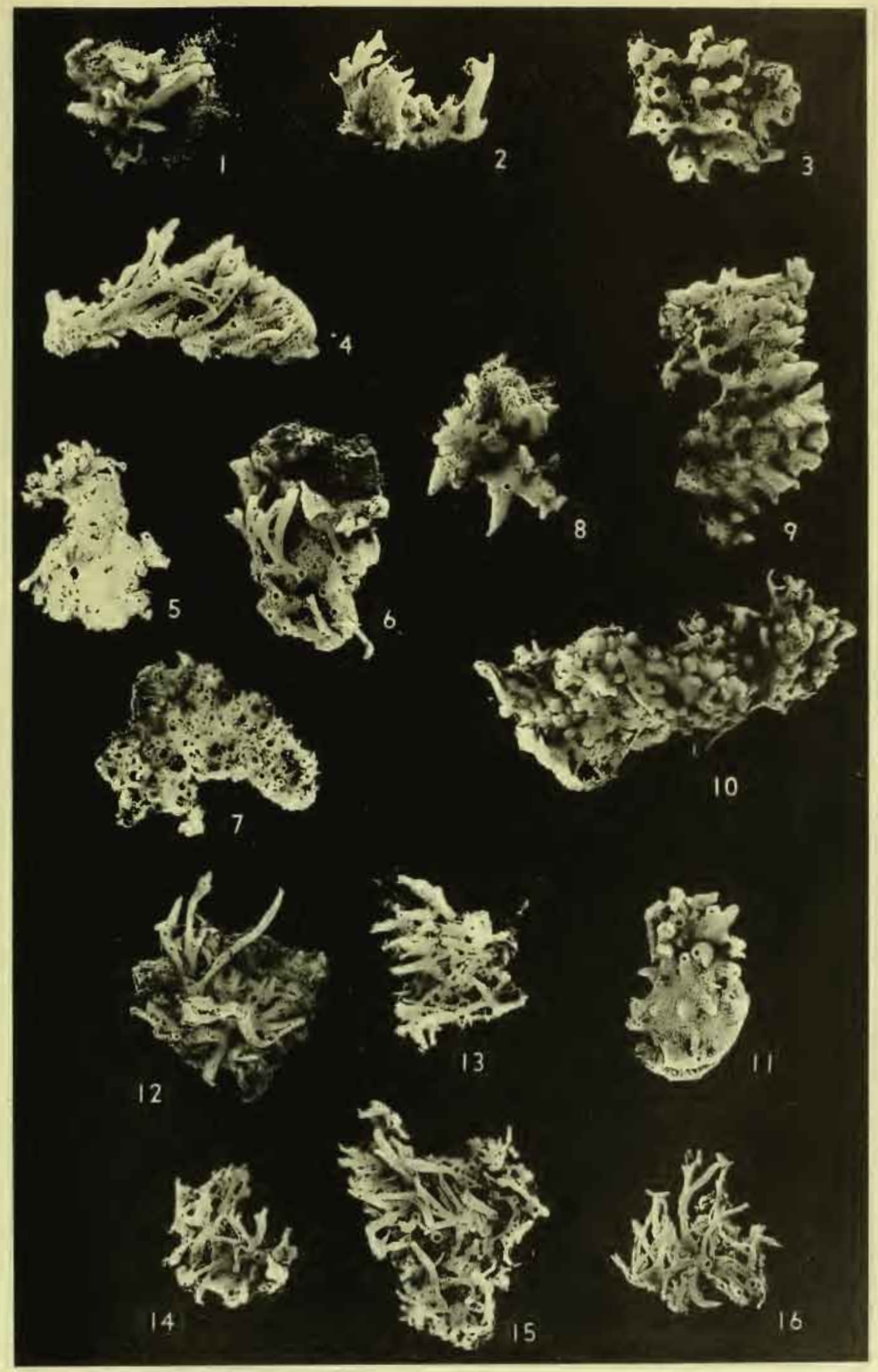
Figs. 4, 6. Colonies with long, horizontal branches partly fused to basal mass; viewed from above. Hammonasset, Conn. YPM #1821. x 3/4.

Figs. 5, 7. Encrusting colonies with low oscular tubules; viewed from above. Hammonasset, Conn. YPM #2023F. x 3/4.

Figs. 12-16. Colonies with long, thin, anastomosing branches; all viewed from above. Fig. 12: Double Beach (Branford), Conn. YPM #1848. x 3/4.

Figs. 13, 14, 15: Double Beach (Branford), Conn. YPM #1838. x 3/4.

Fig. 16: Double Beach (Branford), Conn. YPM #1956D. x 2/3.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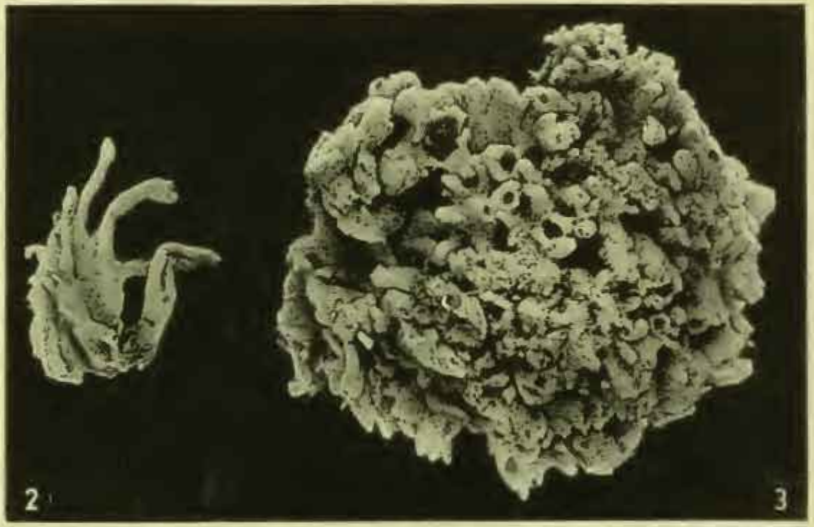
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PLATE 12

Fig. 1. *Haliclona loosanoffi*. Gemmules attached to the shell of a barnacle. Milford Harbor, Conn. YPM #614. x 10. (Alcohol)

Fig. 2. *Haliclona loosanoffi*. Colony with tall, vertical branches; viewed from side. Solomons Isl., Md. YPM #627. x 4/5. (Alcohol)

Fig. 3. *Haliclona loosanoffi*. Typical colony from the Maryland population. Solomons Isl., Md. YPM #627. x 4/5. (Alcohol)

Fig. 4. *Haliclona loosanoffi*. Gemmules from Solomons Island, Md. YPM #627. x 10. (Alcohol)

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