

THE PELAGIC CNIDARIA OF THE GULF OF MEXICO:  
ZOOGEOGRAPHY, ECOLOGY AND SYSTEMATICS

A Dissertation

by

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Submitted to the Graduate College of the  
Texas A&M University in  
partial fulfillment of the requirement for the degree of

DOCTOR OF PHILOSOPHY

May 1972

Major Subject: Biology

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## ABSTRACT

The Pelagic Cnidaria of the Gulf of Mexico:  
Zoogeography, Ecology and Systematics (May 1972)  
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Directed by: Dr. Sewell M. Hopkins

Zoogeographic, ecologic and systematic studies conducted on the pelagic Cnidaria of the Gulf of Mexico revealed 18 species of scyphozoans (including an undescribed species of Nausithoe), approximately 56 species of hydromedusae (including six new species and one new genus) and 45 species of siphonophores. Eight species of siphonophores (Amphicaryon ernesti, A. peltifera, Clausophyes ovata, Maresearsia praeclara, Marrus orthocannoides, Nectopyramis diomedae, N. natans and Praya dubia) previously known only from the Indo-Pacific are reported for the first time for the western Atlantic. Other records of forms previously known only from the Indo-Pacific include the scyphozoans Deepstaria enigmatica and Periphyllopsis braueri as well as the deep water continental shelf hydromedusae Bythotriara depressa and Calycopsis simulans. The hydromedusan genus Halistaura previously known only from three Pacific species now includes a new species from the Gulf of Mexico. East Atlantic medusae reported for the western Atlantic for the first time include the hydromedusae Dipurena ophiogaster, Sarsia gemmifera, Steenstrupia nutans and Zygocanna vagans and the scyphomedusa Atolla vanhoeffeni.

In addition to the well defined bathypelagic cnidarian

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assemblage the Gulf of Mexico cnidarian fauna may be divided zoogeographically into a northern Gulf neritic and estuarine assemblage, which appears to be a Pleistocene relict fauna, and a tropical neritic and epipelagic fauna of the southern Gulf which is primarily of West Indian origin, but includes also some Indo-Pacific and East Atlantic components.

The Carolinian fauna of the northern Gulf was isolated in the Pleistocene from the Carolinian region by the peninsula of Florida. The occurrence of the east Atlantic forms and Pacific forms in the Gulf indicates a previous continuity of the world's tropical waters across the Isthmus of Central America. Isolation of the Gulf of Mexico from the Indo-Pacific probably occurred last in the Pliocene, dividing the fauna into Atlantic and Pacific populations.

Hydromedusae which will serve as indicators of neritic water in the epipelagic have been defined. Northern and southern Gulf species are easily distinguished. Analysis of northern Gulf estuarine and neritic medusae and siphonophores indicate that they are excellent indicators of estuarine flushing and mixing of neritic and oceanic waters. Seasonality in northern Gulf neritic and estuarine leptolinid medusae has also been elucidated and has been found to be primarily temperature dependent.

Quantitative analysis of medusan growth patterns in selected species indicates a wide variety of allometric and isometric growth patterns in closely related and widely divergent forms.

Infraspecific analysis of Bougainvillia carolinensis in the northern

Gulf reveals that neritic and estuarine populations are morphologically distinct.

Examination of cnidarian-symbiont systems revealed metazoan parasites and symbionts including an unusual cestode-like larva parasitic in the cabbagehead jellyfish, Stomolophus meleagris.

Many individuals have aided me in my studies of the pelagic Cnidaria. Drs. Sewell H. Hopkins and Gordon Gunter made this entire study possible and if it were not for them it would never have been initiated and completed. I am much indebted to Dr. Leo Berner, Jr., for allowing me access to the material taken by the R/V ALAMINOS. I would also like to thank the other members of my committee for their encouragement and constructive criticisms. I would very much like to thank Dr. Kalman Horvath (Texas A&M University) for his assistance in collecting Stomolophus and Ouwensia.

Histological studies were greatly aided by Dr. Norman Levin (Department of Biology, Brooklyn College) who collaborated with me on the histological studies of Ouwensia. I am also very grateful for the aid extended me by Dr. Angeles Alvarino (Scripps Institution of Oceanography) in identifying various agalmid siphonophores. Dr. John Grady and other staff members of the National Marine Fisheries Service Laboratory (Galveston, Texas) have my appreciation for allowing me to examine samples taken by the R/V GERONIMO and other NMFS vessels. I would also like to thank many individuals, particularly several of my fellow graduate students at Texas A&M University, for help in obtaining materials and specimens. These individuals are Messers Thom Rennie, Howard Armstrong, Ross Epstein and Douglas Lipka. I also owe thanks to numerous individuals at the Gulf Coast Research Laboratory (Ocean Springs, Mississippi) who aided me in sampling the neritic and estuarine waters of that area. I owe special thanks

to Mr. Charles K. Eleuterius for his aid in critically evaluating the statistical analyses in this dissertation and designing the computer programs and statistical formats used herein.

Support for studies in Mississippi waters were supplied in part by Public Law 89-720 and the State of Mississippi. Additional support was supplied by the Gulf Coast Research Laboratory. Financial support at Texas A&M University for materials was provided by the Department of Biology. The R/V ALAMINOS material was taken with support supplied by Office of Naval Research and the National Science Foundation.

Additionally I owe a great debt to my parents for their unstinting support. My wife Carol deserves special thanks for her patience and fortitude.

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## INTRODUCTION

The major objectives of this study were to determine the species composition of the pelagic cnidarian fauna of the Gulf of Mexico and to determine the zoogeographic affinities of this faunal assemblage. Other objectives were to elucidate distributional patterns in the Gulf and to determine what use, if any, might be made of medusae or siphonophorae as indicators of water masses and currents. The planktonic and pelagic cnidaria included in this report are limited to the Scyphozoa, Hydromedusae and Siphonophorae. Although the chondrophorans Velella velella and Porpita porpita are common in the Gulf they were not considered in this study. Also included in this report are observations on parasites and commensals of pelagic cnidaria of the Gulf of Mexico.

The literature dealing with the planktonic or pelagic cnidaria of the Gulf of Mexico is extremely sparse. With respect to the hydromedusae Moore (1962) published a note on the occurrence of the anthomedusan Nemopsis bachei in Mississippi. Sears (1954a) lists hydromedusae she thought should occur in the Gulf of Mexico, basing her suppositions on Mayer's (1910) monumental work, "Medusae of the World" and other records by Mayer (1900) from near Dry Tortugas. In another paper Sears (1954b) presents a hypothetical list of siphonophores, again none based on actual records, for the Gulf.

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The citations on the following pages follow the style of  
Bulletin of Marine Science.

Both reports by Sears must be discounted. They apply only to the West Indian faunal region. With respect to siphonophores of the true Gulf there have been no substantive publications.

Hedgpeth (1954) made some pertinent observations on the commoner coastal Scyphozoa of Texas, these being Chrysaora quinquecirrha, Stomolothus meleagris, Cyanea capillata, Aurelia aurita and several other species. Hoese *et al.* (1964) discussed the seasonal occurrence of Cyanea capillata at Port Aransas. Sanders and Sanders (1963) erected a subspecies of the mauve stinger (Pelagia noctiluca) calling it P. n. mexicana. Guest (1959) discussed the seasonal occurrence of sea wasps (Chiropsalmus quadrumanus) on the Texas coast. Phillips and Burke (1970) discuss the occurrence and ecology of sea wasps (Ch. quadrumanus and Tamoya haplonema) in Mississippi coastal waters.

Allwein (1967) did a study of the hydromedusae of the North Carolina coast, thus augmenting Brooks' (1882) work on medusae from the Woods Hole region. Vanucci (1957) has done extensive work on coastal hydromedusae of Brazil. Kramp (1959), in his discussion of Atlantic hydromedusae, states that the Gulf of Mexico hydromedusan fauna is virtually an unknown factor in the zoogeography of Atlantic waters.

As is the case with many other groups of marine invertebrates the Cnidaria have received very little attention by zoologists working in the Gulf of Mexico. This is unfortunate not merely from an academic standpoint. Cnidaria, on a purely quantitative

basis, are a major component of the marine zooplankton. The Cnidaria are of distinct biomedical interest in that some extremely noxious and toxic forms are common in Gulf waters (Phillips and Burke 1970), and some forms may indeed constitute a medical hazard under certain conditions. Additionally, Cnidaria are of considerable importance in the trophic structure of Gulf coast estuarine areas (Phillips *et al.* 1968). Some forms may also serve as very useful indicators for quantitating coastal discharge into the surface waters of the oceanic environment (Vanucci 1957 and Alvarino 1968).

## PROCEDURES

### Collections and Ecologic Studies

Cnidaria from neritic and estuarine plankton samples from Mississippi (Figures 1 and 2), Louisiana and Texas coastal waters were analyzed. Isaacs-Kidd midwater trawl samples and meter net samples taken by the R/V ALAMINOS (Department of Oceanography, Texas A&M University) were analyzed for their cnidarian complements. Collection locations and station data for the R/V ALAMINOS collections are given in Figure 3 and Table 1 respectively. Selected stations in Mississippi coastal waters (Figures 1 and 2) were sampled on a monthly basis for twelve to eighteen months. Estuarine samples were taken from March 1968 through February of the following year and the neritic stations (Figure 2) were sampled from October 1967 through January 1969. Mississippi Sound plankton collections were taken with a small surface plankton net (18-inch mouth opening, 30 inches in length) made of 0.33 Nitex. Neritic samples south of Mississippi Sound were made with a slightly larger net (mouth opening 0.5 meter, length 1.5 meters) which was made of 00 mesh nylon. Collection of larger coastal cnidaria was made with dip nets and otter trawls. Additional neritic plankton samples taken by the National Marine Fisheries Service (Galveston, Texas) off the Texas and Louisiana coasts were examined on a purely qualitative basis for confirmatory purposes. Mr. John Grady of the NMFS Oceanography Department at Galveston, Texas, kindly supplied me with cnidaria picked out of a series of Hensen Net samples taken by the

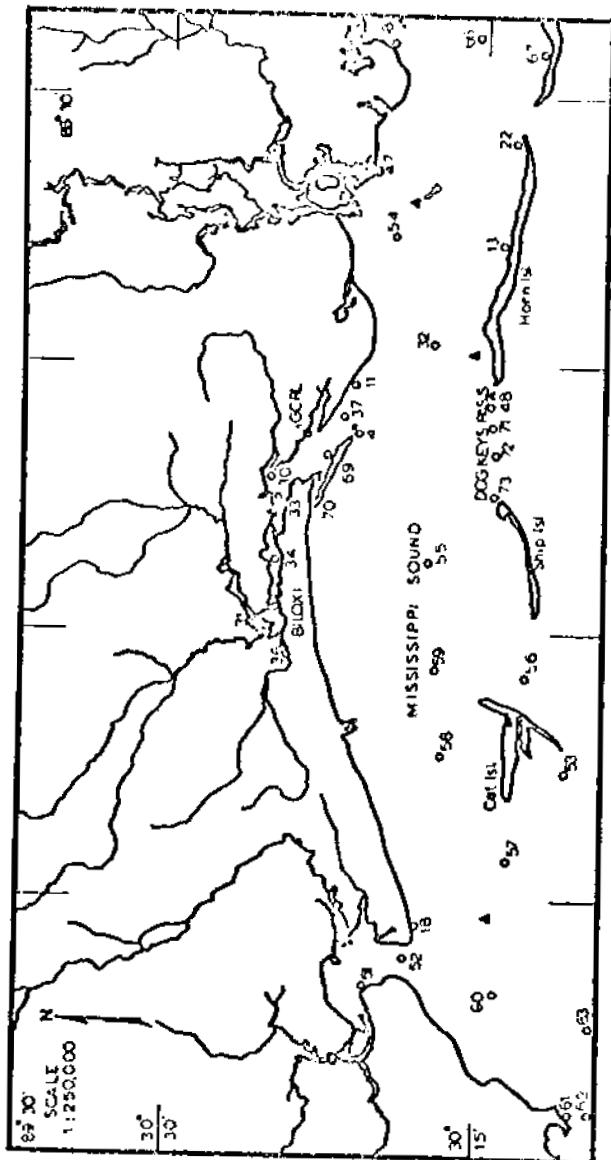
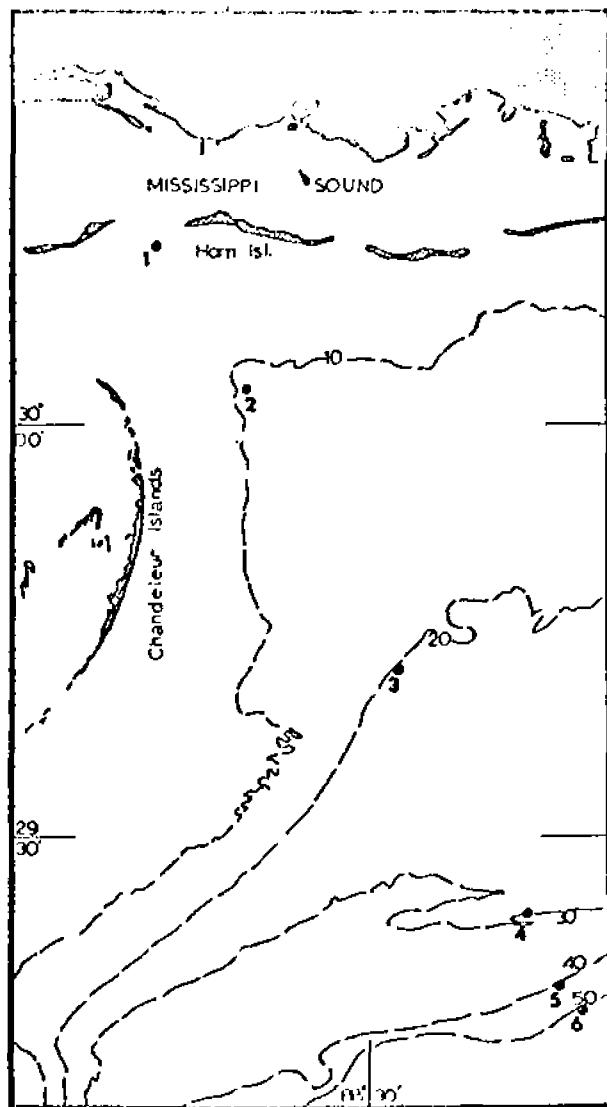


Figure 1. Collecting sites in Mississippi Sound. Solid black triangles indicate dredge sample sites; circles indicate plankton sampling sites.



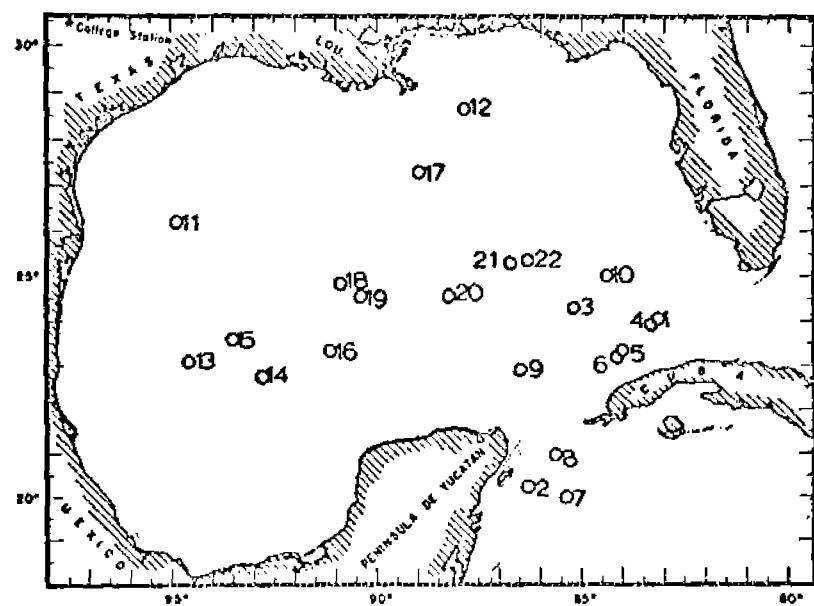


Figure 3. Collecting sites for the R/V ALAMINOS.

TABLE 1  
DATA PERTAINING TO R/V ALAMINOS COLLECTIONS

R/V ALAMINOS			Position		Tow Depth
Collection Number	Reference Number	Date	N	W	(meters)
<b>Meter Net Samples</b>					
1	65A9IV3	3 July 65	24°00'	83°11'	100
2	65A9X12	8 July 65	20°17'	86°17'	100
3	65A9XVIII	13 July 65	24°24'	85°04'	100
<b>Isacs-Kidd Midwater Trawl Samples</b>					
4	65A9III	3 July 65	24°03'	83°07'	0-675
5	65A9V	4 July 65	23°14'	83°59'	0-1875
6	65A9VI	4-5 July 65	23°15'	84°02'	0-2500
7	65A9X	7-8 July 65	19°58'	85°14'	0-2400
8	65A9XIII	9-10 July 65	20°53'	85°35'	0-2600
9	65A9XIV	11 July 65	22°57'	86°21'	0-350
10	65A9XXII	14-15 July 65	24°58'	84°16'	0-1410
11	65A14I	2 Oct. 65	26°17'	94°50'	0-1250
12	66A5V	4 April 66	28°44.5'	87°46'	0-1000
13	66A9II	3 July 66	23°02.5'	94°34'	0-100
14	66A9III	3 July 66	23°21.5'	93°50'	0-750
15	66A9V	4-5 July 66	23°33.5'	93°29.5'	0-900
16	66A9VII	6 July 66	23°21.5'	91°07'	0-2900
17	66A9XVI	12 July 66	27°18'	88°50.5'	500-950
18	69A13VIII	5 Oct. 69	24°53'	90°45'	at 2475 only
	69A13VII	5 Oct. 69	24°53'	90°45'	0-1600
19	69A13XI	6 Oct. 69	24°36'	90°25'	0-2700
20	69A13XV	7 Oct. 69	24°21'	88°11'	650-1100
21	69A13XVIII	8 Oct. 69	25°22'	86°36'	1000-1225
22	69A13XX	8 Oct. 69	25°26'	86°19'	0-350

R/V GERONIMO at scattered localities in the Gulf (Figure 4).

No medusae or siphonophores other than extremely common epipelagic forms were encountered in these latter samples. A quantitative analysis of Mr. Grady's extensive samples which would indeed illuminate much with respect to surface currents in the Gulf is a monumental task by itself and is beyond the scope of this study. Limited dredge sampling (using a small scallop dredge) was conducted in Mississippi Sound (Figure 1) in an attempt to locate scyphozoan polyps. Work on the neritic and estuarine medusae was conducted personally by me when at the Gulf Coast Research Laboratory from 1967 through 1969.

All samples which were initially fixed in 5-15 percent formalin were transferred to saline solution or sea water for 2-24 hrs and then placed in 70 per cent ethanol.

Samples from Mississippi waters were quantitated in the following manner. Each plankton sample was drained and its drained volume determined to the nearest ml. A portion (1-5 ml) of this drained sample was taken for analysis of calycocephoran siphonophore abundance. The numbers of polygastric and eudoxid stages for each species were determined. Although records were kept of the numerical abundance of anterior and posterior nectophores as well as bracts and gonophores, abundance of polygastric and eudoxid stages is defined only in terms of anterior (or definitive nectophores) and bracts respectively. After determination of the abundance of the various stages and species in the aliquot the

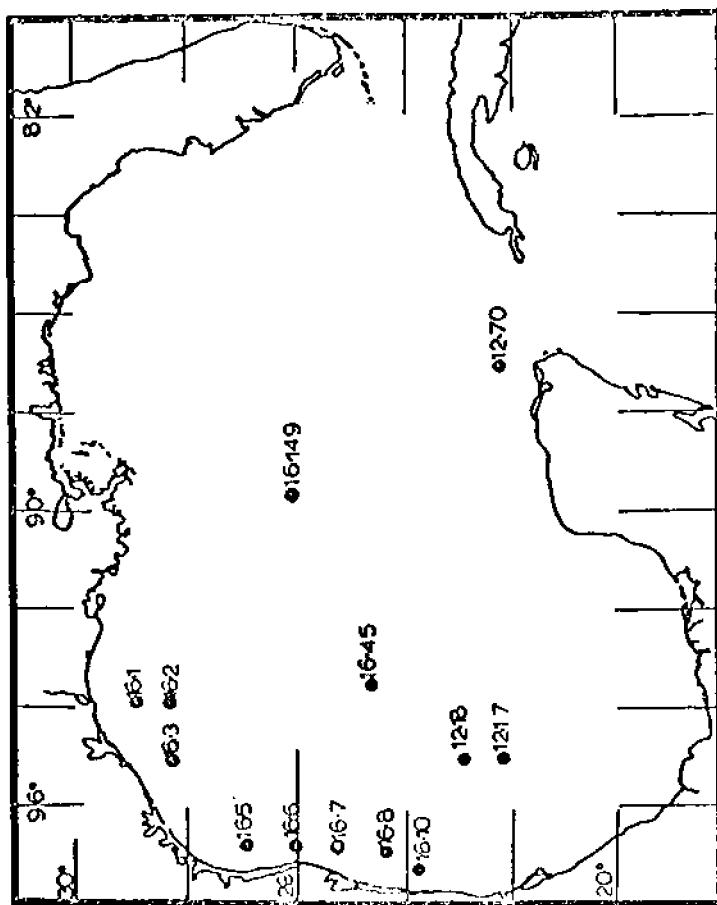


Figure 4. Collecting sites for the R/V GERONIMO.

value was then corrected for the total drained plankton volume. Total samples were analyzed for medusae and cystonectid and physonectid siphonophores. Cystonectid and physonectid siphonophores, because of their extreme fragility, were quantitated only on the basis of pneumatophores or complete nectosomes in the given sample. Unfortunately all Mississippi samples were lost as a result of Hurricane Camille, August 1968.

Midwater trawl samples were not quantitated because of the lack of consistent sampling technique (i.e. varying depths, fishing time and cod end gear). Complete station data for the R/V ALAMINOS collections can be found in Pequegnat and Pequegnat (1970). Hydrographic data in Mississippi Sound and adjacent waters routinely included salinity and temperature determinations. Salinity was measured by using a Goldberg refractometer and water temperature was determined by use of a hand held or reversing thermometer. Unless otherwise noted in the text temperature and salinity values represent surface values.

All specimens were examined for parasites and commensals, and note was made of predator and prey relationships based on field and laboratory observations. An account of the symbionts and trophic relationships is given in the last section of this work.

#### Morphology and Systematics

Classification of medusae follows Kramp (1961) and the systematic arrangement of the siphonophores follows that of Totten (1954 and 1965). Works of extreme value for identification of

medusae include "Ayer (1900, 1910), Kramp (1919, 1926, 1947, 1957, 1959 and 1961), Bigelow's works on medusae of the Atlantic and Pacific Oceans (1909, 1913, 1918, 1919b and 1940) and Russell's classic two volume work (1953 and 1970) "Medusae of the British Isles". Kramp's keys to Atlantic and Pacific hydromedusae along with a diagnosis of each form (1959 and 1968a) are especially helpful. Works valuable in recognition of siphonophores include those by Totton (1954 and 1965), Huxley's (1859) classic "Oceanic Hydrozoa", the "Siphonophora of the Challenger Expedition" by Haeckel (1888), Chun (1891 and 1892), Lens and van Riemsdijk (1908), Bigelow (1911a,b, 1913, 1918, 1919 and 1931) Bigelow and Sears (1935) and Sears (1953).

No names have been applied to new species and genera in this dissertation. Binomials will be applied to newly described species upon publication. Since specimens taken in Mississippi coastal waters were lost in Hurricane Camille, descriptions of Eucheilota n. sp., Octophialucium n. sp. and Halistaura n. sp. will not be valid until more specimens are obtained to serve as type material.

Special emphasis has been accorded the scyphozoan and bougainvilliid medusae, wherein detailed consideration has been given to growth patterns and comparative morphology. Comparative quantitative studies of medusae have seldom been attempted. This type of work, however, is extremely valuable for systematic purposes and provides a somewhat less subjective set of criteria for comparing populations. The comparative quantitative studies on

coastal scyphozoans and bougainvilliids involve comparative analyses of variance for pertinent morphologic features. Regression curves and correlation coefficients for the various parameters are compared. Calculation of statistics utilized follow the methods given by Fraser (1953).

For an extensive treatment of siphonophoran morphology Totton (1954 and 1965) and Garstang (1946) are the most useful works. Russell (1953) is highly recommended for the morphology of hydromedusae and Thiel (1966) and Russell (1970) give excellent discussions of comparative scyphozoan morphology.

All of the drawings in this report were made freehand from preserved material. Photomicrographs were taken using a 35 mm camera back mounted to an appropriate microscope. Specimens were stained for contrast with any of several stains including methylene blue, eosin, Congo red, Bengal red or fast green. Eosin and methylene blue are best for staining calycophoran siphonophores for morphologic study, the stains being easily removed by destaining in acid alcohol.

Measurements of specimens were made with the use of either metric rules, vernier calipers or dividers and are expressed in millimeters unless otherwise noted.

Methodology with respect to parasitological and aquarium studies is discussed in the given section.

## RESULTS AND DISCUSSIONS

A systematic listing of all species taken in this study as well as others previously reported from the Gulf with respective habitat distributions, is given in Table 2. Collection sources for each of the species is given in Table 3. The Scyphozoa, Hydromedusae and Siphonophora are each discussed separately and each group is discussed on an ecological and distributional basis. Morphologic or ecologic accounts of individual species are given where sufficient data are available. Descriptions are given for newly described species only. One new species of coronate scyphomedusa (Nausithoe n. sp.) and six new species of hydromedusae are described. A total of 19 species of scyphomedusae (16 of which were taken in this study), approximately 54 species of hydromedusae and 45 species of siphonophora are known to inhabit the waters of the Gulf of Mexico.

Ecologic studies include an account of the seasonal occurrence of medusae in Mississippi Sound and adjacent neritic waters as well as an account of siphonophore distribution in northern Gulf waters. While the data from the R/V ALAMINOS collections were inadequate for ecologic analysis, information obtained from the collections examined was extremely useful with respect to analysis of cnidarian habitat distribution patterns in the Gulf and for comparing the oceanic fauna of the Gulf with that of other water masses.

An account of pelagic cnidarian host symbiont systems is given after the three cnidarian groups are discussed.

TABLE 2  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Oceanic			
	Estuarine	Neritic	Epipelagic	Bathypelagic
<b>Scyphozoa</b>				
Order Cubomedusae				
Family Carybdeidae				
<u>Tamoya haplonema</u> Muller 1859			N	
* <u>Carybdea aurifera</u> Mayer 1900			N?	
Family Chiropodidae				
<u>Chiropsalmus quadrumanus</u> Muller 1859	N,T		N,T	
Order Coronatae				
Family Atollidae				
<u>Atolla vanhoeffeni</u> Russell 1957			X	
<u>A. wyvillei</u> Haeckel 1880			X	
Family Linuchidae				
* <u>Linuche unguiculata</u> (Schwartz 1893)	N,T		X	
Family Naustithoidae				

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC Cnidaria OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Oceanic		
	Estuarine	Neritic	Epipelagic
<u><i>Nausithoe punctata</i></u> (Kolliker 1893)		N,T	X
<u><i>N.</i></u> sp.			
Family Paraphyllidae	-		
<u><i>Paraphyllina</i></u> sp	N?	X	
Family Periphyllidae			
<u><i>Periphylla periphylla</i></u> (Péron & Lesueur)			X
<u><i>Periphyllopsis braueri</i></u> Vanhoffen 1900			X
Order Semaestomae			
Family Peiagidae			
<u><i>Chrysaora quinquecirrha</i></u> (Desor 1848)	N,T	N,T	
<u><i>Elinia noctiluca</i></u> (Forstkal 1779)	N,T	N,T	X
Family Cyaneidae			
<u><i>Cyanea capillata</i></u> (L.)	N	N	
Family Ulmaridae			
<u><i>Aurelia aurita</i></u> (L.)	N,T	N,T	X

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Estuarine	Neritic	Oceanic			
			Epiipelagic	Bathypelagic		
<b>Order Rhizostomae</b>						
Family Cassiopeidae						
<i>*Cassiopea frondosa</i> (Pallas 1774)	N,T	N,T				
<i>*Cassiopea xamachana</i> R. P. Bigelow 1842	N,T	N,T				
Family Rhizostomatidae						
<i>Rhopilema verrilli</i> (Feukes 1887)		N,T				
Family Stomolophidae						
<i>Stomolophus meleagris</i> L. Agassiz 1862	T	N,T	X			
Incertae sedis						
<i>Deepstaria enigmatica</i> Russell 1967			X			
<b>Hydromedusae</b>						
<b>Order Anthomedusae</b>						
Family Corynidae						
<i>Dipurena ophiogaster</i> Haeckel 1879	N,T					
<i>Sarsia gemifera</i> Forbes 1848	N					

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Oceanic			
	Estuarine	Neritic	Epipelagic	Bathypelagic
<b>Family Tubulariidae</b>				
<u>Hybocodon forbesi</u> Mayer 1894			N,T	
<u>Euphyllora gracilis</u> Brooks 1882	X		N,T	
<u>Stenstrupia murans</u> M. Sars			N	
<b>Family Zancleidae</b>				
<u>Zanclea costata</u> Geyenbauer 1856		N		
<u>Zancleopsis</u> N. sp.		D		
<b>Family Cytaeidae</b>				
<u>Cyrtaeis tetrastyla</u> Eschscholtz 1829		N,T	X	
<b>Family Clavidae</b>				
<u>Oceania armata</u> Kolliker 1893		N,T	X	
<b>Family Hydractiniidae</b>				
<u>*Podocoryne carneae</u> M. Sars		N		
<b>Family Bougainvilliidae</b>				

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Estuarine	Neritic	Oceanic	
			Epipelagic	Bathypelagic
<u>Bougainvillia carolinensis</u> McCrady 1857	X	N		
<u>B. frondosa</u> Mayer 1900		N		
* <u>B. superciliaris</u> L. Agassiz 1862		N		
* <u>B. inaequalis</u> Fraser 1944		N		
* <u>B. rugosa</u> Clarke 1881		N		
<u>B. platyaster</u> (Haeckel 1879)		S	X	
<u>Nemopsis bachei</u> L. Agassiz 1849	X	N		
Family Pandidae				
<u>Amphinema dinema</u> Peron & Lesueur 1809		N		
<u>A. rufosum</u> Mayer 1900		N,T		
<u>Stomotoca pterophylla</u> Haeckel 1879		N,T	X	
Family Calycopsidae				
<u>Calycopsis simulans</u> (Bigelow 1909)		D		
<u>Euthomiara depressa</u> Naumov 1960		D		
Order Leptomedusae				
Family Dipleurosomatidae				
<u>Dichotomia cannoidea</u> Brooks 1903		T		

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Oceanic			
	Estuarine	Neritic	Epipelagic	Bathypelagic
<b>Family Laodiceidae</b>				
<u>Laodicea brevicona</u> Allwein 1968			T	
<u>L. undulata</u> Forbes & Goodsir 1853			N	
<u>Orohistoma pileus</u> (Lesson 1843)		T		X
<b>Family Campulariidae</b>				
** <u>Cbelia</u> spp	X			
<u>Phialidium globosum</u>	X	N		
<b>Family Lovenellidae</b>				
<u>Eucheilota</u> n.s.p.		N		
<b>Family Phialellidae</b>				
<u>Phialella</u> sp	X			
<b>Family Phialuciidae</b>				
<u>Octophialucium</u> n.s.p.	X	N		
<b>Family Eirenidae</b>				

PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Estuarine	Neritic	Oceanic	
			Epipelagic	Bathypelagic
<i>Eirene pyramidalis</i> L. Agassiz 1862	X	N		
<i>Histiocirrha</i> sp.				
Family Eutimidae				
<i>Eutima variabilis</i> McCrady 1857	X			
Family Acquoreidae				
<i>Aequorea floridana</i> L. Agassiz 1852			X	
<i>A. acquorea</i> (Forsskal 1775)			N, T	X
<i>A. persilis</i> (Eschscholtz 1829)			N, T	X
<i>Zygoctina vagans</i> Bigelow 1911			T	X
Order Limnomedusae				
Family Proboscidactylidae				
*** <i>Pochella polynema</i> Harrlaub 1917			N	
<i>Proboscidactyla ornata</i> McCrady 1857			N, T	X
Order Trachymedusae				
Family Ceryonidae				
<i>Cervonia proboscidialis</i>			N	

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Estuarine	Neritic	Oceanic	
			Epipelagic	Bathypelagic
<u>Liriope tetraphylla</u> Chamisso & Eysenhardt 1821	X	N,T	X	
Family Halicreatidae				
<u>Palicreas minimum</u> Fewkes 1882				X
<u>Haliscera bigelowi</u> Kramp 1947				X
Family Rhopalonematidae				
<u>Aclaura hemistoma</u> Peron & Lesueur 1809		N,T	X	
<u>Persa incolorata</u> McCrary 1857		N,T	X	
<u>Rhopalonema velatum</u> Gegenbaur 1856		N,T	X	
<u>Rh. furearum</u> Vanhoffen 1902				X
<u>Colebonema sircium</u> Vanhoffen 1902				X
<u>Crossata rufohruenea</u> (Kramp 1913)				X
<u>Pentachegen haeckeli</u> Maas 1893				X
Order Narcomedusae				
Family Aeginidae				
<u>Aecina citrea</u> Eschscholtz 1829	X	X		X
<u>Aeginura grimaldi</u> Maas 1904				
<u>Salmundella bitentaculata</u> Quoy & Gaimard 1833)	N,T	X		

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Estuarine	Neritic	Oceanic	
			Epipelagic	Bathypelagic
<b>Family Cuninidae</b>				
<u>Cunina fowleri</u> (Browne 1906)		T	X	
<u>C. octonaria</u> McCrady 1857		N,T	X	
<u>C. duplicata</u> Maas 1893		T	X	
<u>C. peregrina</u> Bigelow 1909		N,T	X	
<u>Peanatha martagon</u> Haeckel 1879		T	X	
<u>Solmissus incissa</u> (Fewkes 1886)		X	X?	X
<b>Order Siphonophora</b>				
<b>Suborder Cystonectae</b>				
<b>Family Physaliidae</b>				
<u>Physalia physalis</u> (L)	X	N,T	X	
<u>Rhizophysa filiformis</u> Forskal 1775	N		X	
<b>Suborder Physcnectae</b>				
<b>Family Agalmidae</b>				
<u>Erenna richardi</u> Bedot 1904			X	
<u>Nanomia bijuga</u> Chiaje 1841	N		X	
<u>Analma ckeni</u> Eschscholtz 1825	N,S		X	

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Estuarine	Neritic	Oceanic	
			Epipelagic	Bathypelagic
<u>Halistemma rubrum</u> Vogt 1852		?	X	X
<u>Cordagalma cordiformis</u> Totton 1932		N	X	X
<u>Murru orthocanoides</u>			X	
Family Pyrostephidae				
<u>Bargmannia elongata</u> Totton 1954			X	X
Family Physcophoridae				
<u>Physophora hydrostation</u> Forskal 1776				X
Suborder Calycophorae				
Family Prayidae				
<u>Marescursia praecilara</u> Totton 1954			X	
<u>Amphicaryon acaule</u> Chun 1888		N,T	X	X
<u>A. ernesti</u> Totton 1954		N,T	X	X
<u>A. retifera</u> (Haeckel 1888)		N	X	
<u>Rissoea cymbiformis</u> (Chiaje 1822)		N,T	X	X
<u>Prava dubia</u> (Quoy & Gaimard 1833)			X	X
<u>Nectopyramis diomedae</u> Bigelow 1911				X
<u>N. natans</u> (Bigelow 1911)				X
<u>Hippopodius hippocampus</u> Forskal 1776	X	N,T	X	X
<u>Vorticella pentacantha</u> Kolliker 1853		T	X	

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Estuarine	Neritic	Oceanic	
			Epipelagic	Bathypelagic
<u>Vogtia spinosa</u>				
<u>V. glabra</u> Bigelow 1918		T	X	
<u>V. serrata</u> (Moser 1925)		T	X	
<u>Sulcicellaria quadrivalvis</u> Blainville 1834		N,T	X	X
<u>S. biloba</u> Sars 1846		N,T	X	
<u>S. obumii</u> Lens & Van Riemsdijk 1908		N,T	X	
<u>Leristia campanella</u> Moser 1925		N		
<u>L. subtilis</u> Chun 1886		N		
<u>L. fenvieri</u> (Bigelow 1911)			X	
<u>Muspias kochi</u> Will 1844		N,T		
<u>Cheilophyes appendiculata</u> Eschscholtz 1829	X	N,T	X	
<u>Diphyes dispar</u> Chanissé & Eysenhardt 1821	X	N,T	X	
<u>D. bojanii</u> Eschscholtz 1829	X	N,T	X	
<u>Eudistomides mitra</u> Huxley 1859		N,T	X	
<u>E. spiralis</u> Bigelow 1911		N,T	X	
Family Clausophyidae				
<u>Clausophyes ovata</u> (Kufferstein & Ehlers 1860)			X	X
<u>Cheniphyes multicentata</u> Lens & Van Riemsdijk 1908			X	X
Family Abylidae				
<u>Ceratocymba leukarti</u> (Huxley 1859)		N,T	X	
<u>C. dentata</u> (Bigelow 1918)			X	
<u>C. sagittata</u> Quoy & Gaimard 1827		N,T	X	

TABLE 2 (Continued)  
 PHYLETIC LISTING OF PELAGIC CNIDARIA OF THE GULF OF MEXICO AND HABITAT DISTRIBUTION  
 (N=northern Gulf; T=tropical; D=deepwater continental shelf; ?=uncertain occurrence)

Species	Estuarine	Neritic	Oceanic	
			Epiipelagic	Bathypelagic
<u>Abyla haeckeli</u> Lens & van Riemsdijk 1908			X	
<u>Abulopsis tetragona</u> Otto 1823		N,T	X	
<u>A. eschscholtzii</u> Huxley 1859		N,T	X	
<u>Bassia bassensis</u> Quoy & Gaimard 1833		N,T	X	
<u>Enneagonium hyalinum</u> Quoy & Gaimard 1827		N,T	X	
<b>Order Chondrophora</b>				
<u>Velella velella</u> (L)		N,T	X	
<u>Porpita porpita</u> (L)		N,T	X	

\*Medusa not recorded in present study.

\*\*Due to the extreme systematic confusion in medusae of the genus Obelia no trivial names could be applied. Defenbaugh (1977) lists various species of the hydroid. Systematic criteria for the genus (which contains at least 30 species of medusae alone) require complete revision.

\*\*\*Reported by Mayer (1910) for the Louisiana coast. Not encountered in the present study.

TABLE 3  
OCCURRENCE OF PELAGIC CNIDARIA IN THE COLLECTIONS EXAMINED  
(GERL indicates northern Gulf collections in Mississippi Sound and adjacent waters.)

Species	R/V	COLLECTION OR COLLECTION SERIES																						
		GULF GERONIMO	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Scyphozoa																								
<i>Taruya harlonema</i>		X																						
<i>Chiropsalmus</i>																								
<i>Quadrumanus</i>		X																						
<i>Atolla vanhoefeni</i>																								
<i>A. rivillei</i>																								
<i>Vesithoe punctata</i>		X																						
N. n. st.																								
<i>Parechyllina</i> sp.		X																						
<i>Pediophylaxis</i>																								
<i>Periphylla</i>																								
<i>Periphyllensis braueri</i>																								
<i>Chrysaora</i>																								
<i>Thysanostoma</i>																								
<i>Pectinia noctiluca</i>		X																						
<i>Ceriania carillata</i>		X																						
<i>Anemonia aurita</i>		X																						
<i>Dendrodoa verrilli</i>		X																						
<i>Solidaginaria meleagris</i>		X																						
<i>Dentipora</i>																								
<i>Chondromedusa</i>																								
<i>Porpita porpita</i>																								

X

X

X

X

X

X

X

X

X

X

X

X

X

X

TABLE 3 (Continued)  
 OCCURRENCE OF PELAGIC CNIDARIA IN THE COLLECTIONS EXAMINED  
 (GCRL indicates northern Gulf collections in Mississippi Sound and adjacent waters.)

Species	R/V GCRL GERONIMO	COLLECTION OR COLLECTION SERIES																				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<u><i>Velella velella</i></u>	X																					
Anthomedusae																						
<u><i>Hydroodon forbesi</i></u>	X																					
<u><i>Diputena orbiogaster</i></u>	X																					
<u><i>Sarsia serrifera</i></u>	X																					
<u><i>Eudistoma gracilis</i></u>	X	X																				
<u><i>Styelastruria nutans</i></u>	X																					
<u><i>Ambiserrata dinema</i></u>	X																					
<u><i>A. succosum</i></u>	X																					
<u><i>Stermatocia</i></u>																						
<u><i>pterophylla</i></u>	X																					
<u><i>Oceania armata</i></u>	X																					
<u><i>Zonaria costata</i></u>	X																					
<u><i>Cyrtaxis terrastyla</i></u>	X	X																				
<u><i>Bougainvillia</i></u>																						
<u><i>frenata</i></u>	X																					
<u><i>Bougainvillia</i></u>																						
<u><i>carolinensis</i></u>	X																					
<u><i>Bougainvillia</i></u>																						
<u><i>platynaster</i></u>																						
<u><i>Nemopsis bachei</i></u>	X																					
<u><i>Nautilikeraia n. sp.</i></u>																						
<u><i>Zanclocaesis n. sp.</i></u>	X	X																				

TABLE 3 (Continued)  
OCCURRENCE OF PELAGIC CNTARIA IN THE COLLECTIONS EXAMINED  
(ACRL indicates northern Gulf collections in Mississippi Sound and adjacent waters.)

TABLE 3 (Continued)  
OCCURRENCE OF PELAGIC CYNIDARIA IN THE COLLECTIONS EXAMINED  
(GCRL indicates northern Gulf collections in Mississippi Sound and adjacent waters.)

TABLE 3 (Continued)  
 OCCURRENCE OF PELAGIC CNTDARIA IN THE COLLECTIONS EXAMINED  
 (GCCP indicates northern Gulf collections in Mississippi Sound and adjacent waters.)

Species	R/V GCCP GERMINTO	R/V ALANINOS																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
COLLECTION OR COLLECTION SERIES																							
<i>C. peregrina</i>	X									X													
<i>Lernanthra marginata</i>											X												
<i>Scolinusus incassa</i>												X											
<i>Siphonophora</i>																							
<i>Tunisaria rivularis</i>	X																						
<i>Rhizostysa</i>																							
<i>filiformis</i>	X																						
<i>Acantho okeni</i>	X										X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Scyliorhinus tubrum</i>												X	X	X	X	X	X	X	X	X	X	X	X
<i>Centroscyllium</i>																							
<i>coelolepis</i>	X																						
<i>Narcine hilgendorfii</i>	X																						
<i>Frenna richardi</i>												X	X										
<i>Ammodytes elongatus</i>																							
<i>Phycis</i>																							
<i>Argentinasilvestris</i>																							
<i>Archipinnis aculeatus</i>	X										X	X	X	X	X	X	X	X	X	X	X	X	X
<i>A. aculeatus</i>																							
<i>Varius orthocanthoides</i>																							
<i>Anisotremus</i>																							
<i>reticulatus</i>																							
<i>Varesearia</i>																							
<i>praeclarus</i>																							

TABLE 3 (Continued)  
 OCCURRENCE OF PELAGIC CNIDARIA IN THE COLLECTIONS EXAMINED  
 (GCRL indicates northern Gulf collections in Mississippi Sound and adjacent waters.)

Species	GCRL GERONIMO	R/V ALAMINOS																						
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
<b>Rosacea cumbiformis</b>																								
<i>R. dubia</i>		X																						
<i>Nectocystis</i>																								
<i>Cionidae</i>																								
<i>N. rotata</i>																								
<i>Pinnocodius</i>	X	X																						
<i>hironaeus</i>																								
<i>Spiralia sinosa</i>																								
<i>V. elatiri</i>																								
<i>V. serrata</i>																								
<i>Siliccularia</i>																								
<i>Chetivalvis</i>	X	X																						
<i>S. hirata</i>	X	X																						
<i>S. chuni</i>	X	X																						
<i>Dichves dispar</i>	X	X																						
<i>Dichves boiani</i>																								
<i>Lamellaria carinella</i>	X																							
<i>Lamellaria subtilis</i>	X																							
<i>Conchia forsteri</i>																								
<i>Conchia acchi</i>	X	X																						
<i>Chondrites</i>																								
<i>argenticulata</i>	X	X																						

TABLE 3 (Continued)  
 OCCURRENCE OF PELAGIC CNIDARIA IN THE COLLECTIONS EXAMINED  
 (GCRL indicates northern Gulf collections in Mississippi Sound and adjacent waters.)

Species	GCRL	GERONIMO	COLLECTION OR COLLECTION SERIES																				
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<u>Euxodoides mitra</u>	X	X			X	X								X									
<u>E. spiralis</u>	X	X				X													X				
<u>Clausochyes ovata</u>													X										
<u>Chunichyes</u>																							
<u>multidentata</u>													X	X	X	X							
<u>Ceratochysa</u>																							
<u>leukarti</u>	X													X	X								X
<u>C. societaria</u>																			X				
<u>C. dentata</u>																							
<u>Abyla meckeli</u>												X											X
<u>Abylerosis</u>																							
<u>tropica</u>	X	X			X	X	X	X			X	X			X				X	X		X	
<u>A. eschscholtzii</u>	X	X				X	X	X	X						X	X	X						
<u>Bassia bassensis</u>	X	X			X	X	X	X		X		X		X									
<u>Funerarium</u>																							
<u>hvalinum</u>	X						X	X	X										X				

## Scyphozoa

### General Account

Of the 16 species of scyphomedusae collected in the present study, eight (Tamoya haplonema, Chiropsalmus quadrumanus, Nausithoe punctata, Chrysaora quinquecirrha, Cyanea capillata, Aurelia aurita, Rhopilema verrilli and Stomolophus meleagris) are known primarily from coastal waters (i.e. neritic areas shallower than 60 fathoms). Although one badly damaged specimen of Paraphyllina sp. was taken in Mississippi coastal waters its occurrence there was probably accidental. All known members of the genus Paraphyllina are oceanic and since the present specimen was moribund at time of capture I consider it an accidental component of the coastal scyphozoan fauna in the northern Gulf. The distribution of sea wasps (Cubomedusae) in northern Gulf coastal waters has been discussed by Guest (1959) and Phillips and Burke (1970). The sea wasp Chiropsalmus quadrumanus is an extremely common form in shallow northern Gulf waters. The only other sea wasp definitely known to occur in the Gulf, Tamoya haplonema, is known from three specimens off the Mississippi and Alabama coasts (Phillips and Burke 1970). Darnell (personal communication) reports finding Chiropsalmus quadrumanus in Lake Pontchartrain, Louisiana. Of the coastal scyphozoa sea nettles (Chrysaora quinquecirrha) and the cabbagehead jellyfish (Stomolophus meleagris) exhibit the greatest seasonality and a detailed account of their distribution and ecology is presented. Data regarding the early

development of polyps of the winter jellyfish Cyanea capillata versicolor are presented and discussed.

The oceanic Scyphozoa include Periphylla periphylla, Periphyllonsis braueri, Atolla vanhoffeni, Atolla wyvillei, Pelagia noctiluca, and Deepstaria enigmatica. The neritic medusae Aurelia aurita and Stomolophus meleagris have also been taken out at sea by the R/V ALAMINOS. Pelagia noctiluca (the mauve stinger) occasionally forms dense shoals in northern Gulf coastal waters, at times even entering estuarine waters.

The deep water coronate medusae Atolla vanhoffeni (previously only known from the east Atlantic) and Periphyllopsis braueri (previously known only from Pacific waters) are herein reported for the first time from the western Atlantic. Deepstaria enigmatica known previously only from the Pacific is now known to inhabit the Atlantic.

Although the coronate medusa Linuche unguiculata and the rhizostomes Cassiopea xamachana and Cassiopea frondosa are known to occur in the Gulf (Hedgpeth 1954) they were not taken in the present study. Phillips and Burke (1970) consider Hedgpeth's (1954) record of the cubomedusan Carybdea aurifera to be dubious since according to Kramp (1961) C. aurifera is a doubtful species and since Hedgpeth's record was of a juvenile it is quite possible the specimen was a juvenile of Tanoya. S. H. Hopkins (personal communication) reports seeing Cassiopea sp. in Galveston, Texas coastal waters.

**Individual Accounts**

*Atolla vanhoefeni* Russell 1957

Material. R/V ALAMINOS: Collection 4, four specimens  
 Collection 7, one specimen  
 Collection 8, one specimen  
 Collection 14, one specimen

Diagnosis. Two dark brown pigment spots in each of the gastric ostia and cruciform of stomach distinguish this species from

*Atolla wyvillei*. Diameter ranges from 8.5 to 26.4 mm and bell height from 3 to 10 mm. Although the usual number of tentacles is 20 one teratologic specimen had 21 rhopalia and 21 tentacles.

Distribution. This is the first report of this species in the western Atlantic region. Apparently it has, in the past, been confused with wyvillei, until Russell (1957) established the specific validity of this form. It is probably much more widespread than is indicated by the literature.

*Atolla wyvillei* Haeckel 1880

Material. R/V ALAMINOS: Collection 10, three specimens  
 Collection 12, six specimens  
 Collection 17, one specimen (at depth  
 Collection 500 - 950 m.)

Remarks. The clover leaf shaped stomach and absence of gastric ostial pigment spots distinguish this species from *Atolla vanhoefeni*. Most of the specimens taken are small, ranging from 6.0 to 15.6 mm in diameter. The largest specimen taken (41.2 mm diameter) was taken at a depth of between 500 and 950 m. Depth distribution of the other specimens cannot be determined from the present data;

however, it is not unreasonable to assume this form may be epipelagic in Gulf waters, although according to Mayer (1910) this is primarily a deepwater form. Bigelow (1909), however, records numerous specimens taken in the upper 1000 m of the water column. The small size of the medusae may account for the relatively small number of tentacles (20), the largest medusa captured having only 24 tentacles. The great majority of the specimens obtained are females with even the smallest of the medusae being sexually mature, although possible "subadult" in their morphology.

Distribution. This species is evidently cosmopolitan in geographical distribution (cf. Kramp 1961).

Nausithoe n. sp.

Figure 5

Material. R/V ALAMINOS: Collection 9, one specimen (female)

Description. 18 mm diameter, jelly thick; central disc is flat and lacks radiating furrows; lappets spatulate; 8 gonads sac-like, elongate and twisted (up to 4 mm in length) with up to 20-30 ova per gonad; gastric cirri in four clumps of 15-20 cirri each. One quarter of the bell margin is partially damaged and one of the eight gonads is missing, in specimen.

Diagnosis. This species is distinct from all other members of the genus by virtue of its long, sac-like gonads and the large number of gastric cirri. This species, in terms of gonadal morphology, resembles N. albatrossi (Maas 1897) which is known only from the Gulf of Panama and the coast of Chile. N. albatrossi however is



Figure 5. Nausithoe n. sp., exumbrial view (18 mm diameter).

"35-40 mm wide, 35 mm high" and "each row of gastric cirri (is) composed of about four clusters of about five cirri each" Kramp (1961).

Periphylla periphylla (Peron and Lesueur 1809)

Material. R/V ALAMINOS: Collection 4, two specimens  
 Collection 14, one specimen  
 Collection 16, two specimens

Remarks. The present specimens range up to 35 mm wide and 40 mm high with as many as 14 tentacles. Pertinent morphometric data as well as approximate bathymetric distribution for the present specimens are given in Table 4 below.

TABLE 4  
 COLLECTION DATA FOR Periphylla periphylla TAKEN BY R/V ALAMINOS

Collection	Collection Depth (m)	Number of Specimens	Diameter	Height	Tentacles
4	0-675	2	28	23	14
			28	28	12
5	0-1875	1	35	40	9+
6	0-2900	2	30 30	34 34	12 12

Kramp (1947 and 1968b) discusses the bathymetric distribution and geographic distribution of this form and concludes that Periphylla is bathypelagic in all oceans including the western Mediterranean, but does not occur in the deeper basins of the Arctic Sea. He also states (1968b) that the medusae are produced in continental shelf waters, from which they descend to bathypelagic depths when they mature. This concept is supported by Bigelow (1909)

whose collection data for Periphylla in the Pacific indicate that small medusae (10-80 mm in diameter) are found close to the surface (300 fathoms to surface). In this study the shallowest depth from which Periphylla has been taken is 0-675 m. Since all specimens collected are sexually mature they cannot be regarded as juveniles. The present data, though limited, suggested that younger medusae are found closer to the surface.

Parasites. A tetrphyllidean-like plerocercoid was found in the lappet of one specimen. This is discussed in greater detail in the section on cnidarian host-parasite systems.

Periphyllipsis braueri Vanhoffen 1900

Material. R/V ALAMINOS: Collection 10, fragments  
Collection 21, one complete specimen  
badly torn, c. 100 mm  
diameter

Remarks. The present specimens were greatly torn and damaged by the time I examined them. Only fragments of the gonads were present; the sense organs were all but destroyed and only small fragments of the oral arms were present. The coronal musculature could not be discerned at all. The lappets were damaged but could be recognized as belonging to P. braueri as could the distinct pigmentation of the gastrovascular system.

Distribution. This constitutes the first record of this form in Atlantic waters, having been previously reported by Vanhoffen (1902) from the Indian Ocean and by Bigelow (1909) from off the coast of Peru. The second specimen (R/V ALAMINOS, collection 18) was taken

with an at-depth closing device attached to the cod end of the midwater trawl. The depth of capture was between 1000 and 1225 m. In the first instance where only fragments were taken the MWT fished from 0-1410 m with no closing device being employed. This is evidently a deepwater form seldom encountered in the upper 1000 m of the water column.

*Chrysaora quinquecirrha* (Desor 1848)

Diagnosis. *Chrysaora quinquecirrha* is one of the commonest jellyfish found in Gulf of Mexico coastal waters and is notorious for its noxious sting. *Chrysaora* is often incorrectly referred to as *Dactylometra* L. Agassiz 1862. "Dactylometra" (sensu L. Agassiz) refers to Pelagidae with 40 tentacles and 48 marginal lappets, whereas "Chrysaora" applies to Pelagidae with 24 tentacles and 32 marginal lappets. As has been pointed out by Stiasny (1939) and Kramp (1961) the generic distinctions between these two and the genus *Kuragea* Kishinouye are invalid in that they represent different growth stages, various intergrades being commonly encountered.

*Chrysaora* is distinct from *Pelagia* in that *Chrysaora* has a sessile stage and lappet number in *Pelagia* does not exceed 16. Developmentally *Chrysaora* passes through a metaphyral "pelagia" stage. The trivial characters for distinguishing species of *Chrysaora* as pointed out by Kramp (1961) and Mayer (1910) are quite vague and variable.

Northern Gulf specimens reach a maximum diameter of 130 mm. Marginal lappets are tongue shaped. Lappet number varies from

16-40 with a mean of 32. Tentacle number averages 24 (with a range of 16 to 41). Tertiary tentacles are uncommon. Kramp (1961) lists 250 mm as maximum diameter. Mississippi Sound specimens are highly pigmented with 16 radiating stripes and central pigment spot on apex of umbrella. Degree of pigmentation is variable; several pink Chrysaora stage medusae having been collected on the Texas Coast.

Distribution. On the Atlantic coast of North America this form is found as far north as New England. It is also known from the Philippines, Bermuda, the west coast of Africa, and various portions of the Indian coast.

Morphological Variation. This species is subject to great morphological variability. Gulf of Mexico specimens are compared with adult medusae from the Chesapeake Bay area in tabular form below (Table 5). Data for Chesapeake Bay medusae are from Mayer (1910).

TABLE 5  
COMPARISON OF ADULT *Chrysaora quinquecirrha*  
FROM CHESAPEAKE BAY AND MISSISSIPPI SOUND

	Chesapeake Bay	Mississippi Sound
Bell Diameter	170-190 mm	60-130 mm
Number of Rhopalia	8	8
Number of Tentacles	40	24 (16-41)

TABLE 5 (Continued)  
 COMPARISON OF ADULT *Chrysaora quinquecirrha*  
 FROM CHESAPEAKE BAY AND MISSISSIPPI SOUND

	Chesapeake Bay	Mississippi Sound
Number of Lappets	48	32 (16-40)
Gonad Color	pink (female) yellow-ash gray (male)	white-pink (female) ash gray (male)
Bell Color	milky white or with brown stripes	Highly pigmented with 16 brown radiating stripes and central pigment spot on exum brella.

Regression analyses for bell diameter in relation to tentacle number and lappet number as well as lappet number in relation to tentacle number were performed. These are graphically expressed in Figure 6. As can be seen from Figure 6, there is no correlation between bell diameter and tentacle or lappet number, the number of lappets and tentacles reaching a relatively constant value when medusae are between 10 and 20 mm in diameter. There is, as would be expected, a correlation between number of tentacles and lappets, the number of lappets in approximately a one to one correspondence of lappets with tentacles. The relationship between lappets and tentacles can be expressed by the first order equation  $Y=22.594 + 0.6179X$ , where Y is the number of lappets and X represents the number of tentacles.

Northern Gulf Chrysaora are dioecious. Medusae 60 mm or larger

in bell diameter are sexually mature. Mayer (1910) states that in brackish estuaries sea nettles mature with only 24 tentacles (*Chrysaora* stage) and are pale in color, whereas those in "purer ocean water at the mouth of Chesapeake Bay...develop into the dactylometra condition with 40 tentacles." Almost without exception all sea nettles taken in neritic off Mississippi Sound waters remain in the "chrysaora" stage. Additionally, there being little variation in pigmentation other than degree, I conclude that salinity conditions in Mississippi Sound and vicinity do not affect pigmentation. However, the occurrence of dactylometral forms off the Texas Coast may indicate there are distinct populations in different neritic localities in Gulf waters.

Apparently northern Gulf *Chrysaora* differ significantly from Chesapeake Bay populations in terms of comparative morphometrics and size at which sexual maturity is reached. Unfortunately more detailed information on morphological variation is not available for Chesapeake *Chrysaora*. Smaller size at sexual maturity for Mississippi Sound *Chrysaora* may be a function of faster maturation rates possibly as a result of somewhat warmer temperature regimes or genetic differences in the two populations. Smaller size at sexual maturity in warm water populations of many marine organisms is a common phenomenon. The reasons for this situation are still poorly understood. The same phenomenon is also encountered in Gulf of Mexico *Cyanea capillata versicolor* populations. Anomalous specimens of *Chrysaora quinquecirrha* do occur on occasion.

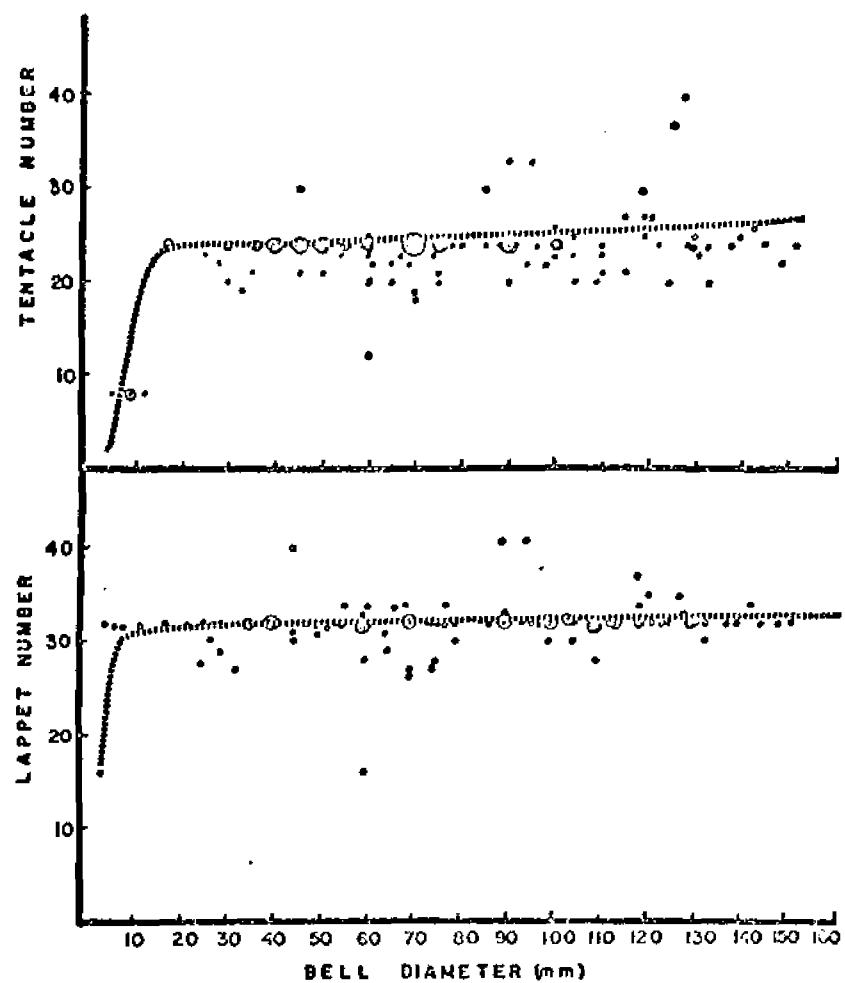


Figure 6. Regression curves for Chrysaora quinquecirrha.

Approximately five percent of all Chrysaora collected (in excess of 900) have either more or less than 16 radiating pigment stripes and a similar number of canals or have three or five gonad pouches. These anomalies may be a result of ephyra condition at time of release.

Ecology. Sea nettles in northern Gulf waters usually make their first appearance as adult specimens in June. During the entire course of the Mississippi Sound study no sea nettle ephyrae or metaephyrae were taken possibly indicating that Mississippi Sound populations resulted during the summers of 1967, 1968 and 1969 from recruitment from other coastal areas. This hypothesis is further substantiated by the fact that no semaeostome polyps were taken in Mississippi Sound. Collection sites from which substrata (mainly oyster shells) were examined for polyps are shown in Figure 1. The size distribution of Chrysaora medusae in Mississippi Sound show no pattern of increasing size during periods of occurrence. The size distributions of different swarms (Figure 7) reflect this very clearly. Similarly there is no pattern of increasing abundance with advancement of the summer months. This is shown graphically (Figure 8) wherein abundance per unit collecting effort during the months July, August And September 1968 is shown. There is absolutely no correlation of number or size with collection date, a situation quite the opposite of that reported by Cargo and Schultz (1966 and 1967) for Chesapeake Bay. Additionally, no semaeostome ephyrae were taken in Mississippi Sound in plankton tows.

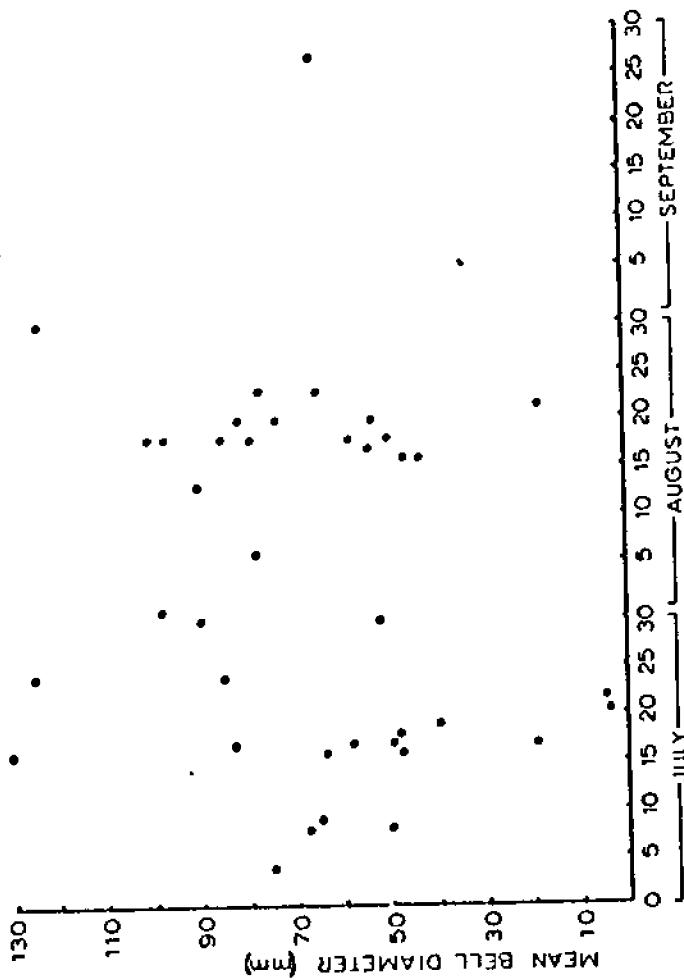


Figure 7. Mean bell diameters of various swarms of *Chrysacta quinquecincta* in Mississippi Sound during the Summer of 1968.

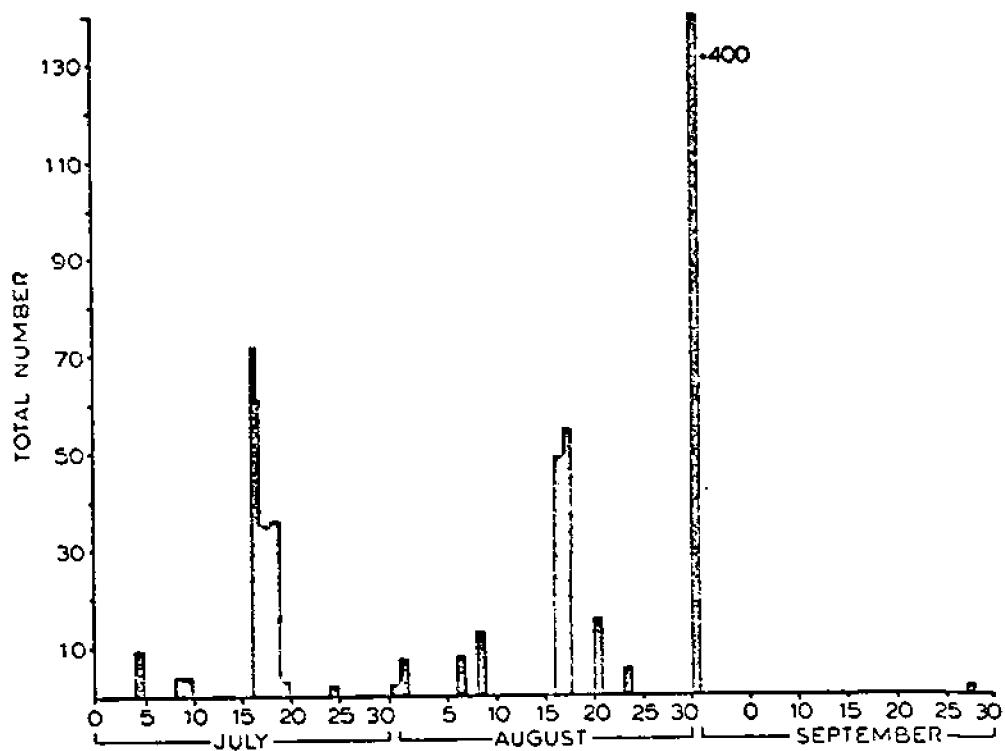


Figure 8. Abundance of *Chrysaora quinquecirrha* in Mississippi Sound during the Summer of 1968.

Although sea nettles were observed on the Galveston, Texas beaches during November and December 1970, none were observed after the first advent of cold weather (late September-early October) on the Mississippi coast. Sea nettles are apparently euryhaline, being commonly taken at salinities varying from 6 to 37 o/oo. The major factor affecting sea nettles in northern Gulf waters apparently is temperature regime. Much more work is needed on the life history of this sometimes quite irritating coastal jellyfish.

Commensals, symbionts, predators and prey of this and other coastal medusae are discussed at length in an earlier publication (Phillips *et al.* 1969).

Pelagia noctiluca (Forskal 1775)

Material. R/V ALAMINOS: Collection 5, fragments of adults  
Collection 8, fragments of adults  
Collection 17, fragments of adults  
Collection 18, fragments of adults

Remarks. Although Sanders and Sanders (1963) consider Gulf of Mexico Pelagia to comprise a distinct subspecies based on very tenuous differences in lappet shape and wart structure I could not differentiate their type material using their subspecific criteria from specimens of Pelagia taken from other tropical waters. Evidently, as in such holoplanktonic hydromedusae as Liriope tetraphylla, particular swarms of medusae may exhibit local differences with respect to particular features, hence the apparent systematic confusion in this genus and the large numbers of invalid species. This has been discussed by Kramp (1961).

Distribution. Epipelagic; ubiquitous in tropical waters and tropical currents.

Ecology. When encountered all sizes may be taken ranging from ephyrae to adults. Sanders and Sanders (1963) state that they collected only adults and no ephyrae or metaephyrae with them. This may be because no plankton tows were taken in the vicinity of the adult medusae. Strong south winds will occasionally cause swarms of Pelagia to be deposited on northern Gulf beaches. Numerous ephyrae and metaephyrae were collected in northern Gulf waters by the R/V RESEARCHER. These forms are high-salinity oceanic forms which become immediately moribund upon entering brackish water.

The presence of only one well defined highly variable species in this genus is characteristic of holoplanktonic groups, speciation in coastal medusae obviously being a function of geographic isolation of sessile stages.

The common name of this species is the "mauve stinger." From my own personal experience the sting from this medusa is considerably stronger and more painful than that produced by the common sea nettle.

Cyanea capillata versicolor L. Agassiz 1862

Distribution. The occurrence of this subspecies in the Gulf was first recorded by Hedgpeth (1954). Mayer (1910) lists it as occurring in swarms between Cape Hatteras, North Carolina and Cape Canaveral, Florida. Hoese et al. (1964) noted the seasonal occurrence at Port Aransas, Texas. Mayer (1910) states that

"they are practically confined to pure open water and do not frequent the harbors." In northern Gulf waters the medusae are commonly taken within the confines of Mississippi Sound during the winter months. Since Cyanea does not occur around the southern tip of Florida, the Gulf population is geographically isolated.

Ecology and Early Polyp Development. Cyanea capillata versicolor were collected in Mississippi Sound during the early spring of 1968 and again during the winter and spring of 1969. On February 11 and 12, 1969 many hundreds occurred in long rows in tide rips. Medusae were collected in Mississippi Sound when salinities were in excess of 20 o/oo and water temperatures ranged between 13 and 16 C. Collection data are given below (Table 6).

TABLE 6  
SALINITY AND TEMPERATURE CONDITIONS AT WHICH  
Cyanea MEDUSAE WERE TAKEN IN MISSISSIPPI SOUND

Date	Temperature (C)	Salinity (o/oo)
4-2-68	14.0	29.6
2-11-69	15.0	27.4
2-11-69	15.0	26.5
2-11-69	14.0	23.2
2-12-69	16.0	27.4
2-19-69	13.0	25.0
3-21-69	16.0	28.2

Most of the medusae observed in February 1969 were denuded of tentacles and oral arms by the fish Poronotus burti (bumpers), dozens of which were observed to associate with a single medusa.

This phenomenon is discussed at greater length by Phillips et al. (1969). Many of the medusae not damaged by associative fishes were found to contain masses of viable planulae.

These adult medusae which were found to be ripe were stripped of the planula complement or held in small tanks until planula release occurred.

Planulae were highly active, of pink to white coloration and about 0.2 mm in length.

Planulae crept or swam on or very near the bottom of the aquaria in which they were placed and settled on the undersides of oyster shells. Encystment usually occurred within 24 hours when a suitable substrate was available, this being shell fragments. Encystment on the underside of shell fragments, a common phenomenon for all semaeostome polyps studied, is not a result of negative phototaxis. This was demonstrated by the fact that planulae kept in darkened aquaria exhibited the same encystment pattern.

Planulae remained active for periods of time exceeding a week in glass tanks wherein no shell fragments were placed.

Cysts are tan or pink, slightly convex discs measuring from 0.10-0.15 mm in diameter (Figure 9). Cyst density on oyster shells were often above 300 cysts per square centimeter.

Within four days after release of planulae four-tentacled polyps were observed. Polyp diameter upon initial emergence from the cyst is 0.15-2.0 mm exclusive of tentacles. A few eight-tentacled polyps of about the same size were found on the same day.

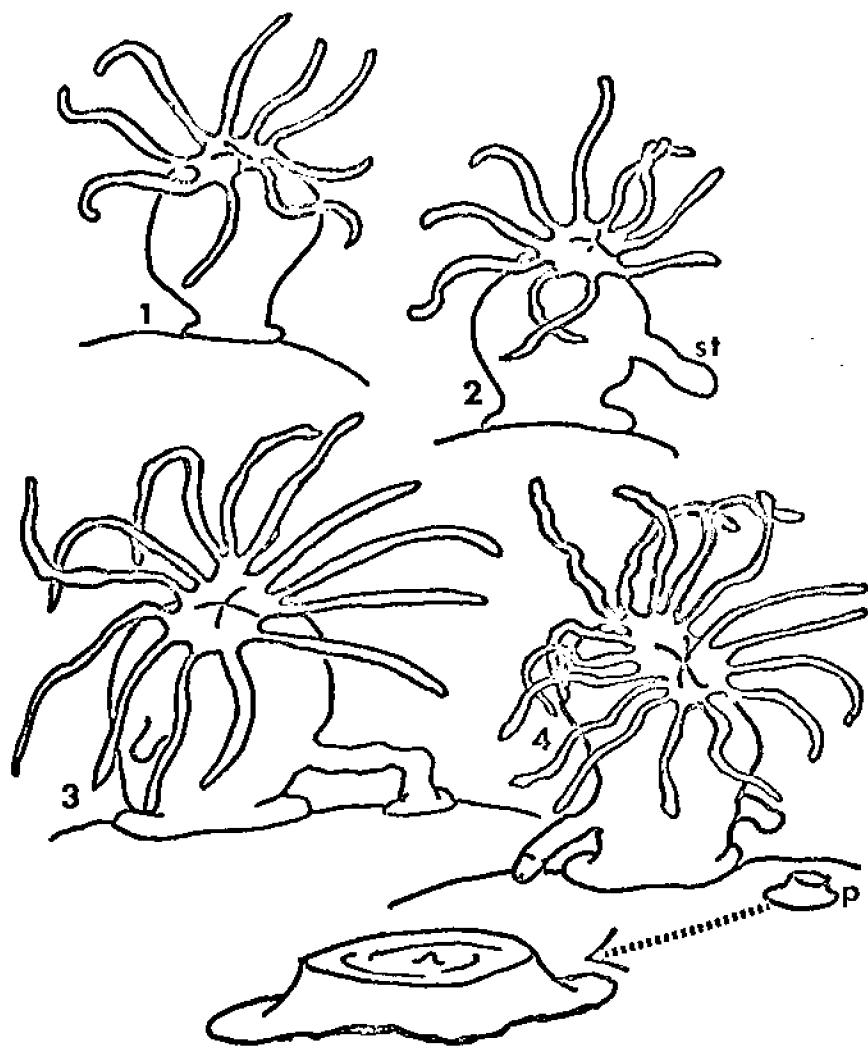


Figure 9. Pedal cyst formation in *Cyanea capillata* polyps. Figures 1 through 4 show progressive outgrowth of a stolon (st) which eventually attaches to the substrate (3) and eventually detaches to form the pedal cyst (p) shown in 4. Pedal cyst structure is shown in greater detail in the inset at end of arrow.

Relaxed polyp height is about 0.2 mm. For a period of about three weeks the developing planulae were maintained on a diet of macerated ctenophore tissue after the technique of Cargo and Schultz (1967). Polyp height within a month following initial excystment is about one mm. At this time the larger polyps were removed from the colonies and isolated in embryo dishes to permit more careful feeding practices and more detailed observations on growth and development. The isolated polyps were routinely given a diet of live brine shrimp nauplii and were examined daily for morphological changes.

Growth is rapid in Cyanea polyps, the ten tentacle stage being attained within 10 days after excystment. The ten tentacle polyp is, exclusive of tentacles, about 1.0 mm high and of 0.5 mm diameter. Polyps from the ten tentacle stage onward actively formed lateral branches or stolons. These stolons initially appeared to secure the developing polyp. Further observations showed that these stolons frequently gave rise to a cyst-like structure which then after varying periods of time (several days to a month or more) gave rise to another polyp. This pedal or secondary cyst is formed by the distal end of stolons near the parent polyp. The anchored stolon separates from the polyp and contracts to a large, dense cyst (Figure 9). The cyst formed differs from the initial cyst in that it is reddish brown, nearly 0.5 mm in diameter, and appears as a concavity with a central papillation.

The 34 tentacle stage can be attained within 50 days after

forms as Glycyrhiza and Cyannea.  
relatively far from coastal areas in conical distribution to such  
that species occurs well into the oceanic waters of the Gulf  
given in Table 7.  
Bell diameters for the R/V ALMINOS material examined are  
four stomach pouches and associated gonads.  
shoe-shaped gonads. These specimens examined here uniformly have  
stranded specimens had only three stomach pouches and three horns  
on the Mississippi Coast. In this instance about a third of all the  
all sizes washed ashore on the south beaches of Horn and Ship Islands  
unprecedented. On 13 December 1966 literally thousands of Aurelia of  
as well as coastal waters. Occurrence of these blooms is somewhat  
Remarks. At time this species occurs in immense swarms in oceanic  
material. R/V ALMINOS: Table 7  
Aurelia aurita (L.)  
nesting nearctic waters.  
quite possibly strobilation and maturation of medusa occurs in  
No Cyannea polyps were encountered in any of the edge samples.  
suggests that strobilation may be a cold triggered phenomenon.  
The appearance of adult Cyannea during late winter and spring  
study.  
is shown in Figure 10. Strobilation was not observed during this  
months. The development and growth of randomly selected polyps  
individually, several acanthular heights of 5-7 mm within three  
intertidal cast emergence. Polyp growth can evidently continue  
nesting.

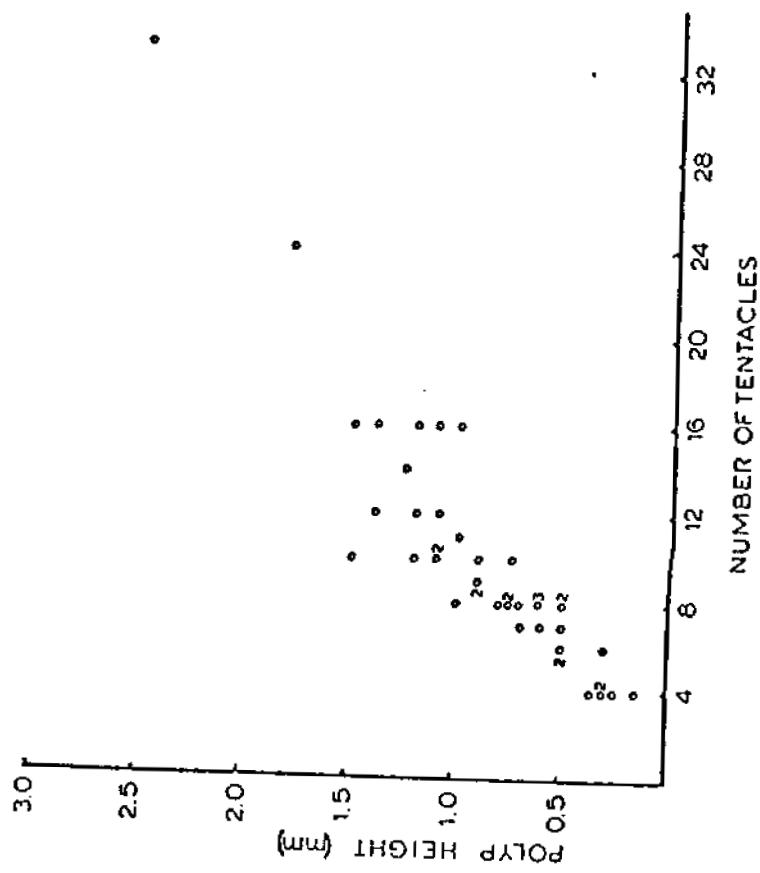


Figure 10. Height of Cyanen polyps at various stages of development.

TABLE 7  
BELL DIAMETERS OF Aurelia aurita TAKEN BY THE R/V ALAMINOS

<u>Collection</u>	<u>Number of Specimens</u>	<u>Diameter (mm)</u>
5	3	200 280 290
11	1	180
12	1	Damaged
14	1	Damaged

Polyps and strobilae of A. aurita are known to occur in Texas coastal waters. These scyphistomae require warm temperatures for strobilation and do not require a period of cold induction necessary for strobilation of A. aurita polyps from New England waters (Spangenberg, personal communication).

Stomolophus meleagris L. Agassiz 1862

Distribution. This species has been previously reported from the Gulf of Mexico by Hedgpeth (1954). According to Kramp (1970) it is exclusively American, being found between 5°S and 25°N in the Pacific and 30°S and 40°N in the Atlantic, its proximity to a given coastal area being a function of warm water currents. Although there are morphological and color differences between the Atlantic and Pacific populations of Stomolophus, both are conspecific.

Ecology. Stomolophus meleagris may be collected in varying numbers year round in northern Gulf waters. Hedgpeth (1954) noted

its extreme abundance at various times of the year on portions of the Texas coast and mentioned its edibility and possible commercial use as a delicatessen specialty item. Feeding behavior and commensals and predators of this jellyfish are discussed at length in an earlier report (Phillips *et al.* 1969). This form is evidently euryhaline and eurythermal being found in significant numbers in Mississippi Sound in salinities as low as 6‰ and at temperatures ranging from 14 to 33°C.

Stomolophus taken in Mississippi Sound range from 3.0 to 380.0 mm in bell height. In Mississippi Sound two size classes are, at times, simultaneously present. Postephyrae are found concurrent with very large adult medusae suggesting that strobilation may occur year round. The polyp has not been found in Mississippi Sound and the ephyra is found only infrequently. The fact that small juveniles are frequently found, however, suggests the possibility that strobilation may occur in the immediate northern Gulf. This species attains its greatest size in spring and winter. Observations on seasonal size variation are given in Table 8.

A number of medusae collected in Mississippi Sound were measured in detail. Measurements taken included bell height, bell diameter and lappet number. The tendency is for maturing medusae of Stomolophus to develop from a somewhat flattened shape to a more globose form with an increase in lappet number. The relationship of bell height (Y) to bell diameter (X) (Figure 11) can be expressed by the equation  $Y = 10.5242 + 0.9953 X$ . The increase in

TABLE 8  
COLLECTION DATA FOR *Stomolophus meleagris* IN MISSISSIPPI SOUND AND ADJACENT WATERS

Date	Number Taken	Mean Bell Height (mm)	Standard Deviation (mm)	Size Range (mm)	Comments
May-June 66	15+	18.26	3.65	14.0-27.00	Early postphyra c.5 mm in bell height found at same time.
18 April 68	1	240.0			<i>S. meleagris</i> ranging in bell height from 100-350 mm found in swash and stranded in shallow water on barrier island beaches.
24 July 68	14	69.85	9.58	57.0-80.0	
24 July 68	1	75.00			
24 July 68	7	79.57	10.39	65.0-95.0	
26 July 68	7	56.25	24.95	35.0-90.0	
31 July 68	12	44.09	22.73	15.0-80.0	
31 July 68	69+	56.55	18.10	15.0-114.0	
31 July 68	5	80.20	9.62	66.0-90.0	
1 August 68	10	61.90	13.80	50.0-90.0	
1 August 68	9	45.55	20.85	26.0-95.0	

TABLE 8 (Continued)  
 COLLECTION DATA FOR Stomolophus meleagris IN MISSISSIPPI SOUND AND ADJACENT WATERS

Date	Number Taken	Mean Bell Height (mm)	Standard Deviation (mm)	Size Range (mm)	Comments
16 August 68	18	32.00	8.23	15.0-45.0	
3 October 68	10	86.50	18.71	60.0-125.0	
9 October 68	9	107.77	13.71	90.0-130.0	
18 October 68	1	2.0			Early postephyra taken offshore.
13 December 68	1+	125.0			Numerous large cabbageheads in swash on barrier islands and coastal beaches.
7 February 69	1	3.0		200-300	Mortalities of medusae of 200-380 mm bell height along coastal and barrier beaches.
24 February 69	1	10.0			Juvenile medusae in estuary.
March 69	100+	c.280		250-380	In swash on most coastal and barrier island beaches.
6 April 69	20+	c.280		200-380	In swash on most coastal and barrier island beaches.

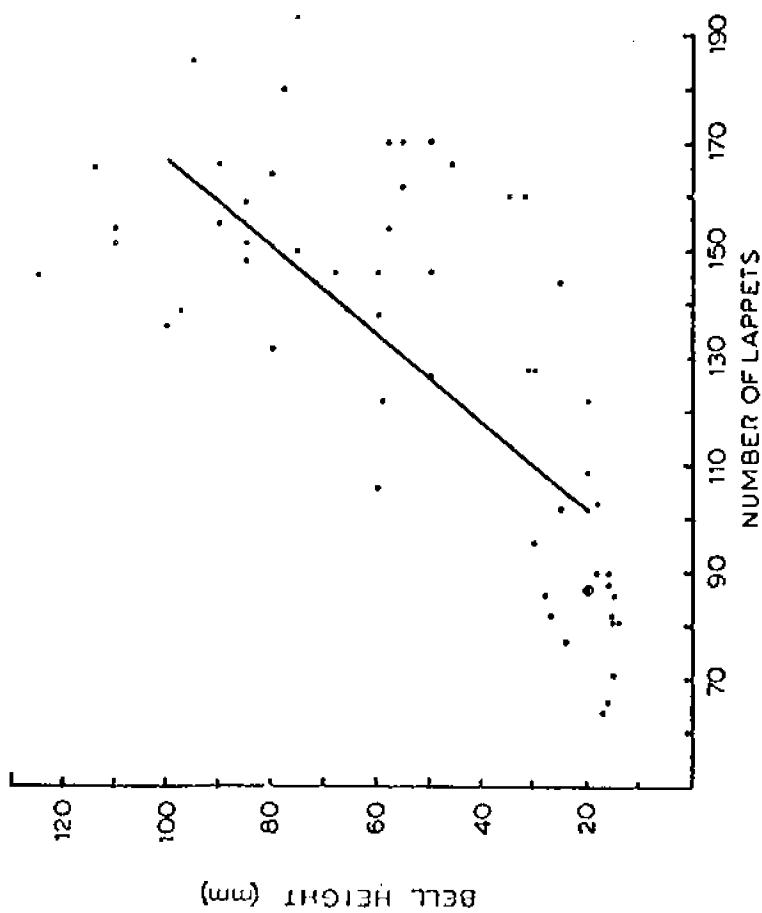


Figure 11. Bell height vs. lappet number in Stomolophus meleagris.

lappet number (Y) with respect to increase in bell height (X) is expressed by the equation  $Y = 86.7210 + 0.7928 X$ . Lappet number is plotted against bell height in Figure 11.

Morphometrics have been taken from field collected specimens of various sizes, growth studies in the laboratory having been precluded by the difficulty of maintenance of Stomolophus in aquaria. When placed in aquaria the medusae produce such copious amounts of mucus as to foul the water and filtration system in very short periods of time.

Rhopilema verrilli (Fewkes 1887)

Material. Eight specimens ranging in bell diameter from 150-600 mm taken in the surf zone of Mississippi Sound barrier islands on the south shores during the months of March, April and May 1968. Unfortunately the specimens and some of the collection data were lost in Hurricane Camille.

Distribution and Zoogeography. Redgpath (1954) reported this form from northern Gulf Coast waters. Mayer (1910) lists it as occurring in various areas of the New England coast, Long Island Sound and North Carolina. Kramp (1970) considers Rh. verrilli to be an obsolete species name, stating that "according to Stiasny (1921 p. 163, as cited by Kramp, 1970) the descriptions given by Fewkes (1887) and Mayer (1910) are erroneous in several respects; it can be taken for granted, therefore, that the genus Rhopilema does not occur in Atlantic waters but is entirely Indo-West Pacific." According to my observations Rh. verrilli is a valid species

occurring in western Atlantic waters. Oddly enough the Atlantic rhizostomatid genus Rhizostoma has not been recorded in Gulf of Mexico waters. Clearly Kramp (1970) is in error with respect to the distribution of the genus Rhopilema.

Deepstaria enigmatica Russell 1967

Material. R/V ALAMINOS: Collection 7, one damaged female, bell diameter in excess of 70 cm.

Diagnosis. The present specimen, although badly torn, is clearly recognizable as D. enigmatica. The anastomosing canal lattice has the characteristic pattern described by Russell (1967). The medusa is a deep purple-blue in color and appears to have had a diameter in excess of 70 cm. The mesogloea is 18 mm thick near the center of the disc. Oral arms are not discernible and portions of the disc are considerably distorted by local extreme contraction. Fragments of the female gonadal material are attached to the subumbrellar surface. These gonadal fragments, too small to permit any observations on gross gonad morphology, did contain zygotes in various stages of early cleavage. Ova and zygotes are small (c. 100  $\mu$  diameter) and have very little, if any, yolk.

Distribution. This is the first report of Deepstaria from the western Atlantic region. This medusa is otherwise known only from the eastern Pacific Ocean where it has been captured via slurp gun by the submersible "Deepstar" over the San Diego Trench and has been taken in midwater trawls by the Scripps Institution of Oceanography Mid Pacific Expedition (Barham and Pickwell 1967).

The depth at which this jellyfish was taken cannot be stated with any certainty since the collecting device fished from the surface to a depth of 2400 m, no "at depth" closing device having been used.

The occurrence of this unique scyphomedusa in the Atlantic constitutes a considerable range extension. Closer examination of midwater trawl samples from other regions and more extensive sampling will probably lead to the discovery of more specimens of Deepstaria from other areas. I strongly suspect that D. enigmatica may have a much more extensive tropical and subtropical distribution. As is the case with many oceanic organisms the zoogeographic distribution of this medusa can probably be correlated with intensity or technique of sampling, and availability of a biologist able to identify it.

All specimens of Deepstaria collected to date, including the present specimen, have been moribund or damaged when collected (Russell 1967 and Barham and Pickwell 1969). It is not clear whether damage of the present specimen is a result of the midwater trawl or whether it was moribund at time of capture. Since large medusae of other species (e.g. Pelagia) also come up badly mangled in the same collecting device I suspect the former possibility.

### Hydromedusae

#### General Account

Approximately 56 known species of hydromedusae occur in the Gulf of Mexico. Of these 54 are recorded in the present study. Of these five are new species. Additionally 2 species previously known from Pacific waters (Bythotiora depressa and Calycopsis simulans) and 3 species previously known only from the eastern Atlantic (Dipurena ophiogaster, Sarsia gemmifera, and Stenstrupia nutans) were taken.

The hydromedusae are most easily discussed by considering the neritic and oceanic faunae individually. The neritic fauna is composed primarily of leptolinid forms which are found primarily in water shallower than 100 fathoms. Since there have been very few neritic samples taken in southern Gulf waters the present account of neritic medusae is limited to the northern Gulf. Some neritic forms have been taken by the R/V ALAMINOS in the southern Gulf, but these are discussed for the sake of convenience with the oceanic fauna. Excluding the cosmopolitan trachymedusae and narcomedusae and the bathypelagic species the Gulf of Mexico hydromedusan fauna is distinctly divisible into a northern Carolinian fauna and an equatorial tropical fauna. The approximate geographic limits of these faunae in the Gulf are shown in Figure 12.

#### Oceanic and Tropical Gulf Hydromedusae

The trachymedusae and all the narcomedusae with the exception of Cunina fowleri (which is known from no area other than the Gulf and West Indian faunal regions) are of little zoogeographic interest

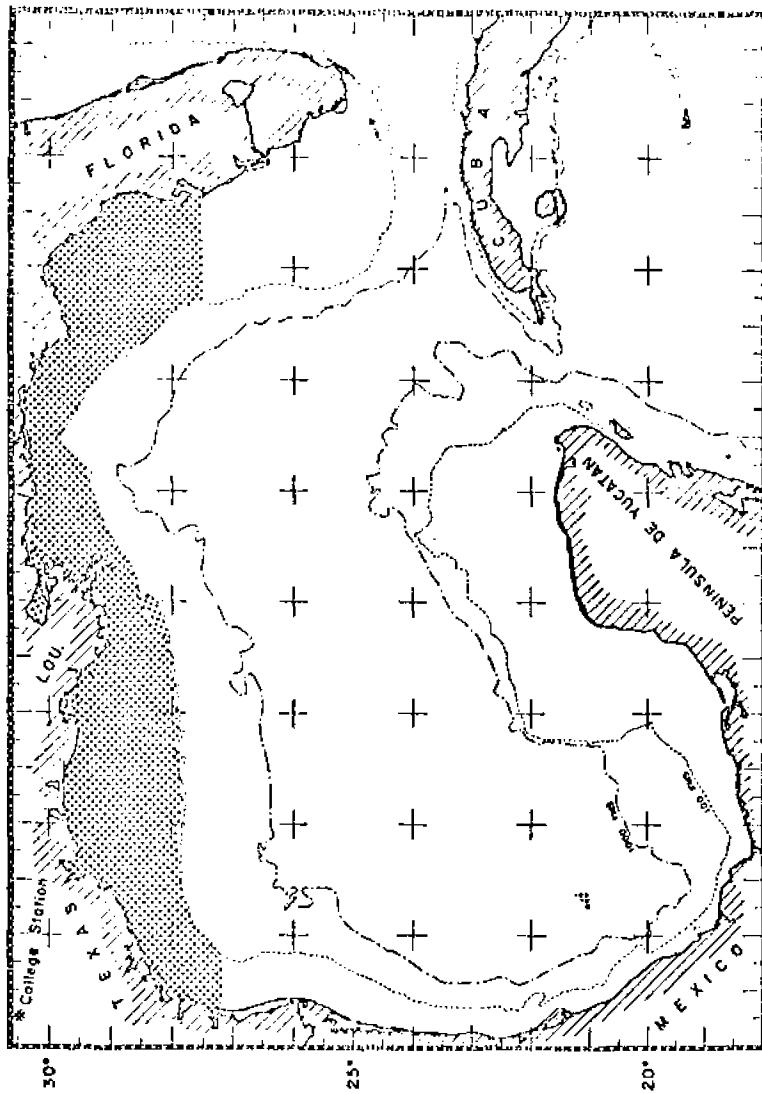


Figure 12. Division of the Gulf of Mexico into northern temperate and southern tropical faunal regions. Stippled area indicates north temperate region.

since these are either cosmopolitan in the deeper water masses or circumglobal in tropical and subtropical waters. Of the 10 species of trachymedusae encountered in the present study, Liriope tetraphylla, Aglaura hemistoma (Figure 13), Persa incolorata (Figure 14), and Phonalonema velatum are ubiquitous epipelagic forms in the warm water masses of the world and can be found in any marine plankton sample taken in the Gulf. Although Geryonia proboscidalis is a tropical form with a wide distribution (Kramp, 1959) it has been encountered only on one occasion and only in the northern Gulf. Halicreas minimum, Haliscera bigelowi, Rhopalonema funerarium, Colobonema sircuum, Crossota rufobrunnea and Pantachogon haackeli are cold water, bathypelagic forms found in all great oceans. Their occurrence in the Gulf indicates that a well developed bathypelagic cnidarian fauna is present. These latter forms were taken only in midwater trawl samples which had fished at bathypelagic depths. Although the surface and epipelagic cnidaria of the Gulf are comparable in many respects to those of the Mediterranean, the Mediterranean lacks a bathypelagic fauna as a result of the shallow sill in the straits of Gibraltar (Ekman 1953). These bathypelagics may be indicative of deep, cold water currents flowing through the Gulf. More intensive sampling with the Isaacs-Kidd midwater trawl and examination of the bathypelagic Cnidaria should be very useful in studying deep water currents in the Gulf. The present collections of course, are inadequate for quantitative evaluation. Bigelow (1909) in his discussion of Pacific medusae pointed out the

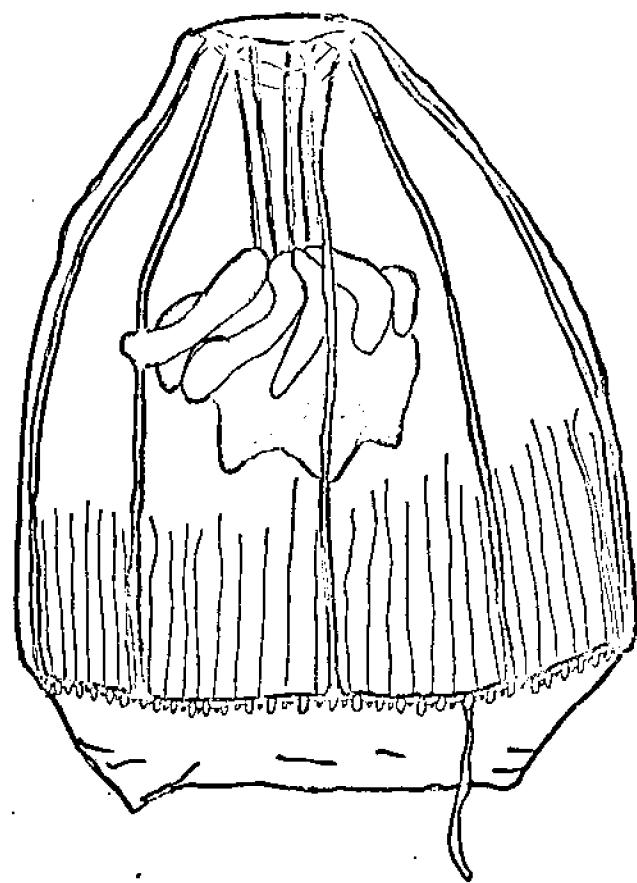


Figure 13. Aglaura hemistoma (2 mm bell height).

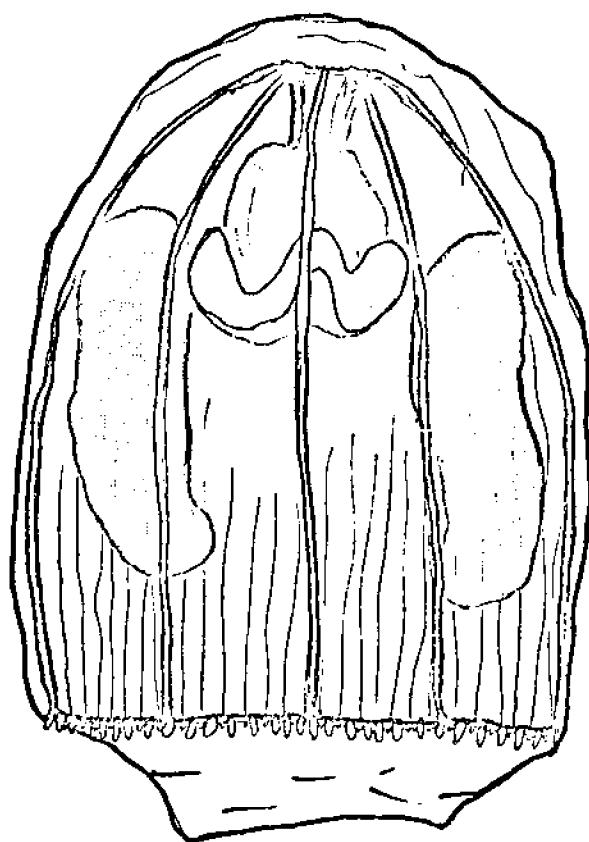


Figure 14. Persa incolorata (2 mm bell height).

value of these deepwater forms as indicators of upwelling in the Central Pacific. However, no attempt has been made since to use these species in a study of upwelling or of coldwater currents.

Among the narcomedusae Aeginura grimaldi is the only widely distributed bathypelagic form found in the Gulf. The remaining species are widely dispersed in temperate and tropical seas.

Solmundella bitentaculata, Cunina octonaria and Cunina peregrina are most common in neritic Gulf waters and their distribution in northern Gulf waters is discussed in the following section.

More significant zoogeographically than the trachy- and narco-medusae are the deepwater shelf species and the epi- and mesopelagic leptolinid medusae. The occurrence of Sarsia gemmifera, Dipurena ophiofaster, Steenstrupia nutans, and Zygocanna vagans, species previously known only from the eastern Atlantic, gives us significant range extensions.

The occurrence of the deep water shelf species Koellikerina n.sp. in the Gulf, which is closely related to the eastern Atlantic K. fasciculata is certainly further evidence of the faunal continuity of the east Atlantic and the Gulf of Mexico and the entire West Indian faunal region.

The presence of deep water shelf species Bythotriara depressa and Calycopsis simulans, two species previously known only from the Pacific, certainly indicates a Pacific origin of at least some of the Gulf cnidarian fauna.

Other than the aforementioned species, the epipelagics and

deep water shelf species, the oceanic-tropical fauna of the Gulf of Mexico is distinctly West Indian-West Atlantic (sensu Kramp 1959).

**Northern Gulf Hydromedusae: Ecology, Seasonal Variation and Zoogeographic Relationships**

The general pattern of occurrence in Mississippi Sound is shown in Table 9. Seasonality in offshore neritic waters is shown in Table 10. There were considerably fewer species (14) in Mississippi Sound than were taken at collecting stations outside of the barrier islands (in excess of 26). As can be seen from Table 11 showing the occurrence and relative abundance of medusae and siphonophores in both the offshore neritic and estuarine areas, only two species, Helgicirrha sp. and Phialella sp., were not recorded outside the estuary. Essentially the hydromedusan fauna of Mississippi Sound is a depauperate shelf fauna characterized by extreme seasonal flux with respect to species composition and population levels as can be seen in Tables 9, 10, and 11.

The most abundant forms in the estuary are Nemopsis bachei (Winter and early Spring), Bougainvillia carolinensis (Spring and Summer), Phialidium globosum (Spring and Summer) and occasional summer blooms of Turritopsis nutricula. There is an extreme paucity of leptolinid medusae during the autumn months. During spring and summer Liriope tetraphylla becomes locally abundant in the estuary. Liriope is the only trachylinid capable of inhabiting Mississippi Sound. Nemopsis and Phialidium occur at times in such dense shoals that they clog plankton nets and trawls. I discussed

TABLE 9  
OCCURRENCE OF HYDROMEDUSA BY MONTHS IN MISSISSIPPI SOUND

Species	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
<u>Douglasinella</u>												
<u>carolinensis</u>	X	X	X	X	X	X	X	X	X	X	X	X
<u>Nemopsis bachei</u>	X	X										
<u>Turritonopsis</u>							X	X				
<u>nuttallula</u>												
<u>Phalidium</u> sp.												
<u>Plebia</u> sp.				X	X	X	X	X	X	X	X	X
<u>Helicirrhiza</u> sp.							X	X	X	X	X	X
<u>Eutima variabilis</u>				X	X	X	X	X	X	X	X	X
<u>Lecoriahalicum</u> sp.							X					
<u>Oncarena ochroaster</u>								X				
<u>Entoloma</u> sp.				X	X	X	X	X	X	X	X	X
<u>Archispora gracilis</u>				X	X	X	X	X	X	X	X	X
<u>Trichella</u> sp.				X	X							
<u>Leptopeltis nutans</u>									X	X	X	X
<u>Leptopeltis tetraphysa</u>									X	X	X	X

TABLE 10  
OCCURRENCE OF HYDROMEDUSA BY MONTHS IN NORTHERN GULF WATERS ADJOINING MISSISSIPPI SOUND

	1967			1968			1969-											
	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2
<u><i>Nemopsis bachei</i></u>		X																
<u><i>Eirene pyramidalis</i></u>							X						X					X
<u><i>Rougainvillia</i> sp.</u>		X	X				X	X	X			X	X	X				
<u><i>Rougainvillia carolinensis</i></u>		X										X						
<u><i>Rougainvillia frondosa</i></u>											X							
<u><i>Ptilidioides globosum</i></u>					X						X	X	X					
<u><i>Anthonema</i> sp.</u>						X								X	X			
<u><i>Eutina variabilis</i></u>		X										X	X	X	X	X		
<u><i>Rhopalonema velatum</i></u>					X							X	X	X	X			
<u><i>Persia incolorata</i></u>												X	X	X				
<u><i>Aclania hemistoma</i></u>												X	X	X	X			
<u><i>Litiozete tetraphylla</i></u>		X	X									X	X	X	X	X		
<u><i>Soleniella bitentaculata</i></u>		X	X									X	X	X	X	X		

TABLE 10 (Continued)  
OCCURRENCE OF HYDROMEDUSAE BY MONTHS IN NORTHERN GULF WATERS ADJOINING MISSISSIPPI SOUND

	1967				1968				1969									
	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2
<u>Sarsia prolifera</u>	.												X		X			
<u>Diphydium ophiogaster</u>													X					
<u>Cyaneis tetrastyla</u>							X	X	X	X			X	X	X	X	X	
<u>Octophialucium</u> sp.													X					
<u>Eirene vidula</u>									X									
<u>Proboscidactyla ornata</u>		X							X	X			X	X	X	X	X	X
<u>Fusheilota</u> n. sp.	X								X			X	X	X		X		
<u>Cunina peregrina</u>									X									
<u>Cunina octonaria</u>	X											X	X	X	X			X
<u>Steenstrupia nutans</u>	X	X	X	X	X	X	X											
<u>Euphyllora</u> sp.			X						X			X		X				
<u>Euphyllora gracilis</u>	X	X			X		X	X	X	X	X	X	X	X	X	X	X	X
<u>Laodicea brevirostra</u>												X	X					
<u>Laodicea undulata</u>												X	X					
<u>Archinema dinema</u>									X			X	X	X	X			

TABLE 11  
FAUNAL CHECKLIST INDICATING RELATIVE ABUNDANCE OF PLANKTONIC  
CNIDARIA IN MISSISSIPPI SOUND AND ADJACENT WATERS

Species	Estuarine	Shallow neritic (5-50 fathoms)
<u>Abyla trigona</u>		X
<u>Abulopsis eschscholtzii</u>		XXX
<u>Abulopsis tetragona</u>		XXX
<u>Aequina sp.</u>		X
<u>Aequorea spp.</u>		X
<u>Agalma okeni</u>	X	XX
<u>Aglaaura hemistoma</u>		XX
<u>Amphinema dinema</u>	X	XX
<u>Amphinema rupestrum</u>		X
<u>Amphicaryon spp.</u>		X
<u>Aurilia aurita</u>	X	X
<u>Bassia bassensis</u>		XXX
<u>Beroe ovata</u>	XXX	XX
<u>Bougainvillia spp.</u>	XXX	XXX
<u>Ceratocymba sagittata</u>		X
<u>Ceratocymba leuckartii</u>		X
<u>Chelophyes appendiculata</u>		XXX
<u>Cordagalma cordiformis</u>		X
<u>Cunina octonaria</u>		XXX
<u>Cunina peregrina</u>		X
<u>Cyanea capillata</u>	XX	XX
<u>Cyaneis tetrastyla</u>		X
<u>Cyaneis sp.</u>		X
<u>Diphyes bojani</u>		XXX
<u>Diphyes dispar</u>	X	XXX
<u>Diporena ophiogaster</u>	X	XX
<u>Eirene pyramidalis</u>		XXX
<u>Euchelota n. sp.</u>		X
<u>Eudoxoides mitra</u>		XX
<u>Eudoxoides spiralis</u>		XXX
<u>Euphyllora gracilis</u>	X	XX
<u>Eutima variabilis</u>	XX	X
<u>Gervonia proboscidea</u>		X
<u>Haliastrella rubrum</u>		X
<u>Haploclirrua sp.</u>	X	X
<u>Heterotihya anonyma</u>		X
<u>Hippomedus hippopus</u>	XX	XXX
<u>Laodicea brevipinna</u>		XX
<u>Laodicea undulata</u>		XX
<u>Lensa campanella</u>		X
<u>Lensa subtilis</u>		X

TABLE 11 (Continued)  
FAUNAL CHECKLIST INDICATING RELATIVE ABUNDANCE OF PLANKTONIC  
Cnidaria in Mississippi Sound and Adjacent Waters

Species	Estuarine	Shallow neritic (5-50 fathoms)
<u>Lensis</u> sp.		X
<u>Liriope tetraphylla</u>	XXX	XXX
<u>Muggiaea kochi</u>	XX	XXX
<u>Manomia bijuga</u>	X	XX
<u>Nemopsis bachei</u>	XXX	X
<u>Obelia</u> spp.	XXX	X
<u>Oceania armata</u>		X
<u>Octophialucium</u> n. sp.		X
<u>Paraphyllina</u>		X
<u>Pegantha</u> sp.		X
<u>Pelagia noctiluca</u>	X	XX
<u>Persa incolorata</u>		XX
<u>Phialellia</u> sp.	X	
<u>Phialidium globosum</u>	X	X
<u>Physalia physalis</u>	XXX	XXX
<u>Porpita porpita</u>	X	X
<u>Praya</u> sp.		X
<u>Proboscidactyla ornata</u>		XX
<u>Rhizophysa filiformis</u>		X
<u>Rhopalonema velatum</u>		X
<u>Rhopilema verrilli</u>	X	X
<u>Rosacea</u> sp.		X
<u>Sarsia prolifera</u>		X
<u>Salmundella bitentaculata</u>	X	XX
<u>Stenstrupia nutans</u>	X	X
<u>Stomolophus meleagris</u>	XXX	XXX
<u>Stomotoca pterophylla</u>		X
<u>Sulculeolaria biloba</u>		X
<u>Sulculeolaria chuni</u>		X
<u>Sulculeolaria quadrivalvis</u>		XX
<u>Sulculeolaria</u> sp.		XX
<u>Vogtia glabra</u>		X
<u>Zanclea costata</u>		X

X = rare (less than 10 specimens from all samples analyzed)  
XX = common (up to 100 specimens from all samples analyzed)  
XXX = extremely abundant (more than 100 specimens from all samples analyzed)

the significance of these species in an earlier paper (Phillips et al. 1969). Moore (1959) discussed the patchiness and extreme local abundance of Nemopsis in Mississippi Sound. During the spring and summer Phialidium replaces Nemopsis. The total population levels of hydromedusae in the estuary on a monthly basis are shown in Figure 15; peak populations occur in late winter and midsummer.

Environmental limits for the estuarine populations are shown in Table 12. Of the fourteen species considered, only Nemopsis bachei, Bougainvillia carolinensis and to a lesser extent Phialidium globosum can be considered eurythermal and euryhaline. This conclusion is based on the observation that these medusae are viable and quite normal looking when collected at the apparent extremes of their salinity and temperature ranges. Although data in Table 12 give the impression that Liriope tetraphylla and Euphyllora gracilis are euryhaline and eurythermal, this is erroneous in that at the lower levels of their apparent temperature and salinity regimes they are typically moribund. The two latter medusae as well as Dipurena ophiogaster and Steenstrupia nutans are "accidental" inhabitants of the estuary in that they are most probably produced in offshore neritic waters and passively carried into the sound by neritic inflow through the barrier island passes.

The major factor affecting estuarine medusa abundance in Mississippi Sound is temperature variation. Water temperature in the estuary drops as low as 11 C during winter and reaches occasional summer extremes of 34 C. At all times water temperature

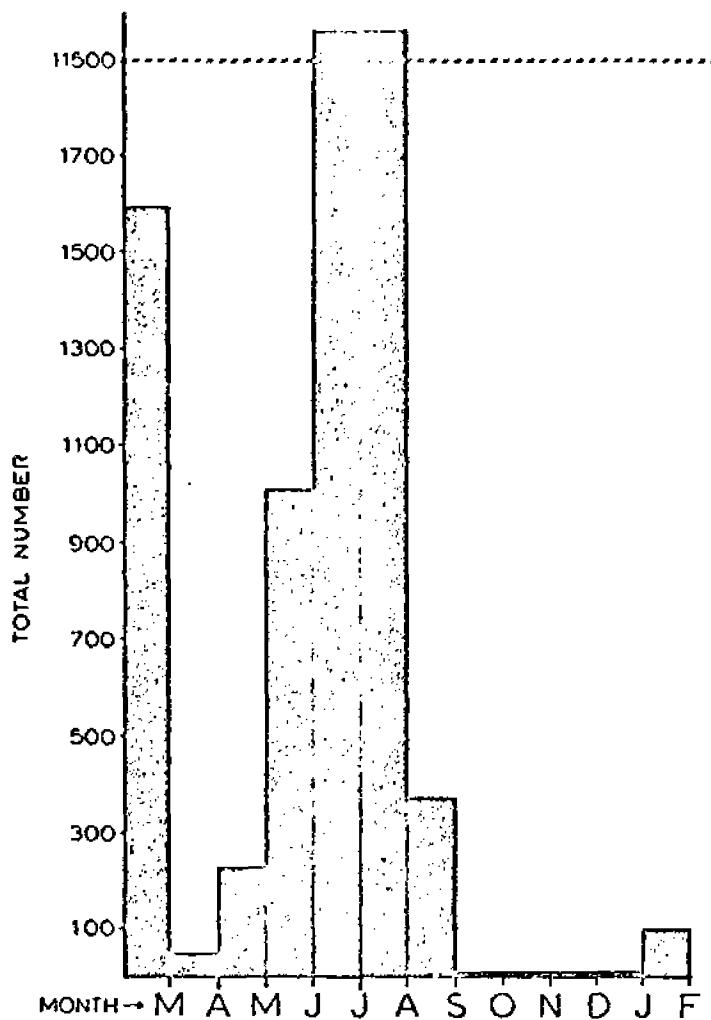


Figure 15. Monthly abundance of hydromedusae in Mississippi Sound. Figures indicate total catch in plankton for each month. The period covered is from March 1967 through February 1968.

TABLE 12  
SALINITY AND TEMPERATURE EXTREMES FOR MISSISSIPPI SOUND HYDROMEDUSAE

Species	Temperature (C)		Salinity (o/oo)	
	Low	High	Low	High
<u>Nemopsis bachei</u>	14	27	6	35
<u>Bougainvillia carolinensis</u>	21	33	16	36
<u>Territopsis nutricula</u>	26	32	23	27
<u>Phialidium</u> sp.	21	33	12	27
<u>Obelia</u> sp.	21	31	23	27
<u>Eutima variabilis</u>	26	32	21	28
<u>Sirene</u> sp.	21	27	23	25
<u>Liriope tetraphylla</u>	24	33	18	31
<u>Euphyllora gracilis</u>	14	33	23	34

in the estuary is subject to short term, local fluctuations depending on wind conditions and amount of rain runoff. Seasonal appearance of leptolinid medusae is probably related to temperature dependent maturation and medusa release. A sudden decline in numbers is probably a function of temperature change to a suboptimal level. Allwein (1967) states that "...the hydrozoan life cycle is directly influenced by temperature. While the number of hydromedusae in a given species may vary from year to year, the medusae of the species are generally released during the same months and are in the plankton for approximately the same period each year. There are apparently optimal temperatures for each species which trigger medusa formation and release."

In some respects the hydromedusan fauna of Mississippi Sound is comparable (at least in terms of seasonality and small numbers of species) to that reported by Allwein (1968) for Helsingør, Denmark and that reported for Cochin, India by Vanucci et al. (1970). Allwein (1968) accounted for the small number of species (19) found at Helsingør as being a result of sheltered waters and a lack of warm water currents which might bring southern species to Denmark's eastern shore. In contrast to Mississippi Sound, Helsingør has much more stable hydrographic conditions. In the case of Mississippi Sound extreme seasonal temperature flux is apparently the major limiting factor for most species whereas the limiting factor at Helsingør is a combination of geographic isolation and the absence of warm water currents. In both areas the

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hydroid fauna is also poor.

In coastal areas where seasonal occurrence of medusae has been studied on at least a semiquantitative basis (and these have been few indeed) there is one major or dominant limiting factor affecting the great majority of species. Vanucci *et al.* (1970) discusses the effects of monsoon flooding on coastal medusae in the Cochin area of India. As would be expected the rapid changing of salinity during the year, in spite of relative temperature stability, is the major hydrographic factor affecting medusa populations. Although drastic local salinity changes in Mississippi Sound may be important in the distribution of local swarms of medusae, it is not nearly as important as seasonal temperature changes and their effects on medusa release and mortality.

The pattern of seasonal occurrence for the North Carolina coast is very similar to that in the northern Gulf. If it were not for the large winter bloom of Nemopsis in Mississippi Sound, seasonal population levels for both regions would be quite similar. In contrast to Allwein's study at Beaufort only 14 species of hydromedusae were taken in Mississippi Sound whereas Allwein reported 37 species from inshore areas. Allwein also reported a total of 55 shelf species for the North Carolina coast whereas a total of only approximately 40 species were taken in northern Gulf continental shelf waters. Qualitative examination of 70 plankton samples supplied by NMFS taken off Louisiana and Texas failed to extend the species list compiled for Mississippi coastal areas.

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The faunae of the two areas, the northern Gulf Coast and the North Carolina coast, are quite similar. It is interesting to note that Laodicea brevignona Allwein 1967 has also been recorded in the present study only in northern Gulf waters. This may represent a "relict" population in the northern Gulf.

In comparison with the North Carolina fauna there are fewer leptolinid forms in the northern Gulf shelf area. When compared to other, more southerly coastal areas of the Gulf (see zoogeography section), northern Gulf coastal waters have a very small number of tropical forms. This is probably due to lower winter temperature maxima in northern Gulf coastal waters. Many of the temperate leptolinid forms in northern Gulf waters may be relict Pleistocene populations cut off from more northerly Atlantic populations by the elevation of the peninsula of Florida. The occurrence of Euchelliota n.sp. and Octophialucium n.sp. in the northern Gulf probably resulted from this geographic isolation. A similar situation exists with respect to populations of the scyphozoans Cyanea capillata versicolor, Aurelia aurita and Chrysaora quinquecirrha.

Mississippi Sound is not comparable with inshore areas near Beaufort, N. C., in that Mississippi Sound is subject to very rapid temperature and salinity changes depending on wind shift and runoff. A strong north wind will drastically alter water level and lower temperatures overnight in Mississippi coastal areas. The waters of the Sound are also much more turbid and support a relatively sparse hydroid fauna.

In terms of holoplanktonic forms such tropical elements as Aeginia citrea, Gervonnia proboscidea, Oceania armata, and possibly Bougainvillia platygaster represent occasional or accidental occurrences in northern Gulf waters. These species, absent from North Carolina coastal waters, represent the only connections with the tropical southern Gulf elements. Although there is much less seasonal temperature fluctuations in offshore northern Gulf coastal waters than in the estuary the habitat is distinctly North Temperate and faunistically distinct from the remainder of the Gulf coastal areas. The North Temperate or Carolinian faunistic affinities of the northern Gulf cnidarian fauna are supported by Defenbaugh (1970, unpublished thesis) in his study of Texas coast hydrozoa.

**Individual Accounts****N. g. et n. sp. incertae sedis**  
Figure 16

Material. R/V ALAMINOS, Collection 7, one specimen (holotype)

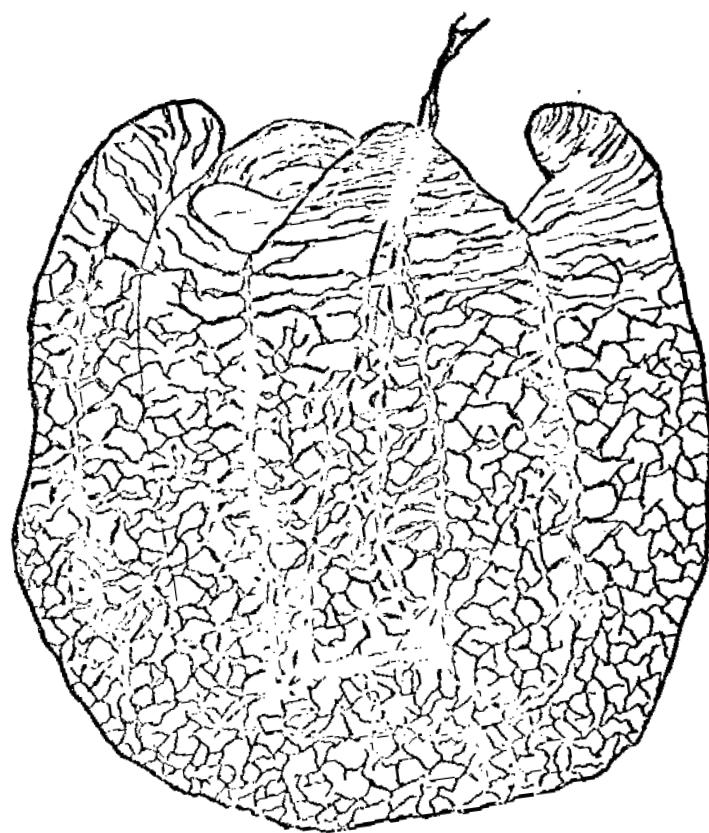
Description of the Genus. The genus is characterized by the highly reticulated anastomosing branches of the four radial and four interradial canals and the fine crenulations of the umbrella which follow the canal branches. The canals do not meet at the apex of the umbrella and a ring canal is absent. There are four well developed marginal lobes.

Species Description. Bell size is 4.2 mm high and 4.0 mm wide. The jelly is thick and firm. There is an apparent manubrium which projects just beyond the bell margin. The terminus of the manubrium, however, is damaged. At the base of the manubrium there is a ring of gonadal tissue. A peduncle is absent. There are no traces of a velum. The medusa is colorless. Tentacles are absent.

Discussion. The canal structure, in terms of the branching and anastomoses, is unique for the hydromedusae. In many respects the canal system is very reminiscent of that found in Ctenophora, especially the Beroidae. Clearly the present specimen is not a ctenophore as witnessed by the lack of an apical sense organ and by the presence of a manubrium like structure with a ring of gonadal material. However, in terms of the canal structure this form is clearly intermediate between the Hydrozoa and Ctenophora.

**Zancloopsis n. sp.**  
Figures 17 and 18

FIGURE 16. *N. g. sp.*, incertae sedis (Hydrozoa). Bell



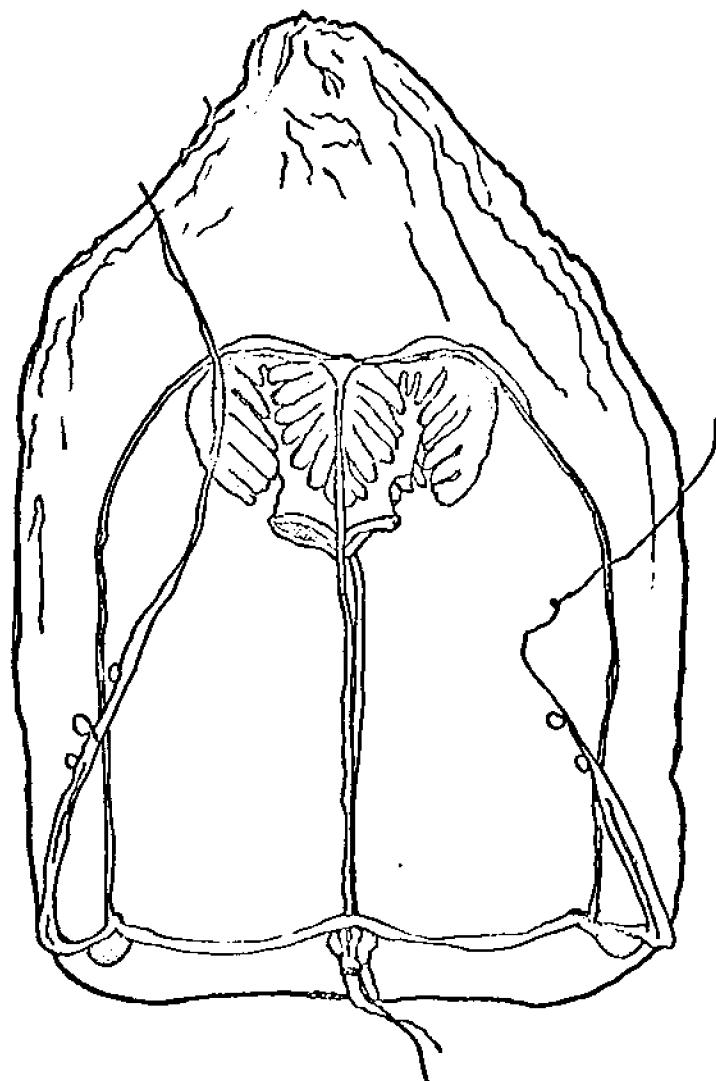


Figure 17. Zancleopsis n. sp. holotype. Bell height is 22.5 mm.

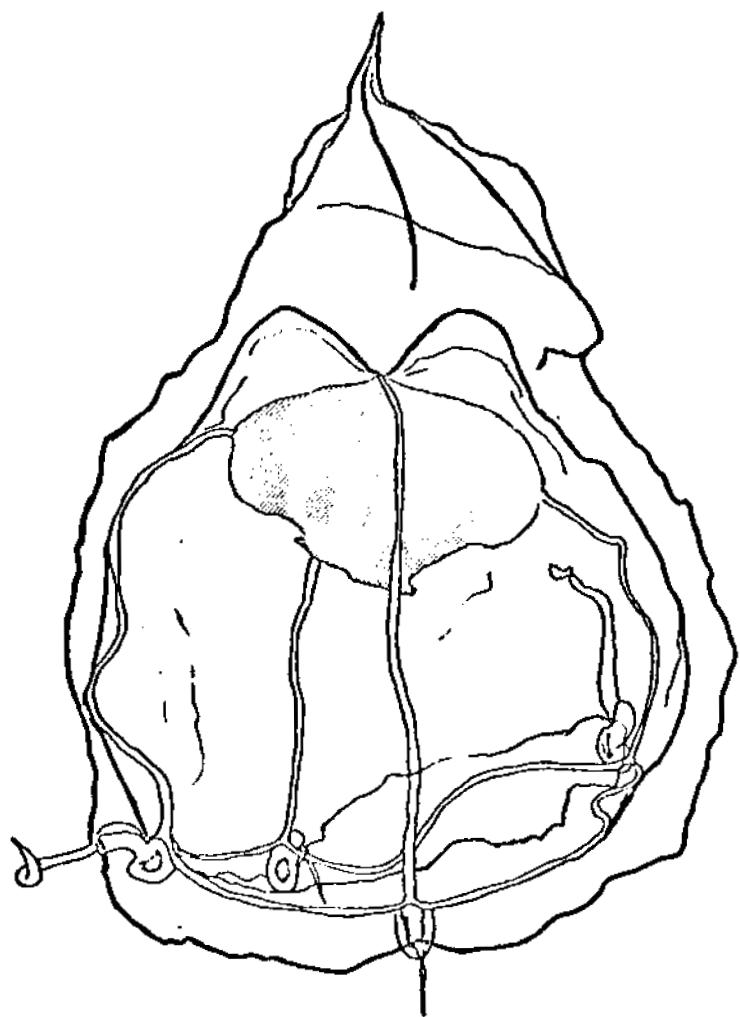


Figure 18. Zancloposis n. sp. juvenile. Bell height  
is 8.5 mm.

Material. R/V ALAMINOS: Collection 2, one juvenile (paratype)  
Collection 7, one adult (holotype)

Description. The gonads are perradial, attached to the base of the stomach and divided by a furrow into two adradial portions each with seven to nine transverse folds. The stomach has four distinct lips. Exumbrial nematocyst tracts extend from the bell margin to the top of the gelatinous conical apical protrusion. Abaxial ocelli are present on the tentacle bulbs. The specimen is laterally compressed. There are two well developed opposite tentacles each, with three globular branches. The remaining tentacles are much shorter and lack the side branches. The well developed tentacles are separated by the width of the laterally compressed bell. The tentacle bulbs are a bright orange in color and laterally compressed.

The juvenile paratype (Figure 18) (8.5 mm high) is similar to the adult morphologically except for the absence of developed gonads, size, and absence of lateral compression. Both specimens appear to have the same, in excess of nine, exumbrial nematocyst tracks and in both the jelly is relatively thick and firm.

Pertinent morphometrics for the two specimens are given in Table 13.

Discussion. The generic criteria for the genus Zancleopsis should be enlarged to include forms with exumbrial nematocyst tracks such as the one described here. I see no reason for erecting a new genus merely on the basis of the presence of exumbrial nematocyst armature. The genus Zancleopsis now has a total of four species, this being the second species from the Atlantic. The four species are compared in tabular format (Table 14). Kramp (1968b) states that

TABLE 13  
PERTINENT MORPHOMETRICS OF *Zancleopsis* n. sp. TYPE SPECIMENS

Feature	Holotype	Paratype
Bell Height (mm)	22.5	8.5
Bell Width (mm)	15.5	6.5
Bell Cavity		
Height (mm)	13.6	5.0
Stomach Height (mm)	4.2	2.2
Stomach Width (mm)	7.8	3.1

TABLE 14  
COMPARATIVE MORPHOLOGY AND ZOOGEOGRAPHIC DISTRIBUTION OF THE  
MEMBERS OF THE GENUS Zancleopsis

	Bell Height (mm)	Bell Width (mm)	Mouth Shape	Gonad Condition	Exumbrial Nematocyst Tracts	Distribution
N.SP.	22.5	15.5	Four lips	7-9 transverse folds	present	Yucatan Basin
<u>gotoi</u>	8	4	No lips	smooth, simple	absent	Japan, East Australia, Nicobars, Madagascar and north Atlantic
<u>tentaculata</u>	25	14	Four lips	Vertical folds	absent	Kei Islands, Samoa Islands
<u>dichotoma</u>	3	2.5	Four lips, small	Interradial	absent	Bahamas, Florida

the two Indo-Pacific species may be identical with the Atlantic  
Zancleopsis dichotoma.

Distribution. The distribution of the four species is given in  
Table 14 along with a comparison of pertinent morphologic features.

Zancleopsis n.sp. most closely resembles the Samoan Z. tentaculata  
in terms of mouth structure, size and tentacle morphology. It  
differs in gonad morphology, the gonads in tentaculata being  
arranged in vertical folds, not horizontal folds as in Z. n.sp.  
Also Z. n.sp. has exumbrial nematocyst armature which is not found  
in the other three species. Although the small Zancleopsis dichotoma  
found in the Bahamas and Florida waters somewhat resembles the  
adult of the new species in terms of gonad and tentacle structure  
it lacks the distinctive apical cap found in both adult and  
juvenile of the present species and has a circular mouth rim.

Z. dichotoma reaches sexual maturity earlier than the present species  
as attested to by the small size of dichotoma (3 mm high, Kramp  
1959). In my estimation the four species are definitely distinct  
and the genus may well have had a Pacific origin as witnessed by  
the present distribution. A Pacific origin is suggested by the  
absence of the genus Zancleopsis from the eastern Atlantic.

Since this species was taken in a meter net near the surface  
it is reasonable to conclude that this is an epipelagic organism.

*Halistaera* n. sp.

Material. R/V RESEARCHER: Station 4 (Figure 2),  
one specimen, March 26, 1968

Description. Diameter is 6 mm and the bell is hemispherical with a thick jelly. The quadrangular manubrium is very short and wide. The manubrium is attached to the subumbrella along the arms of a perradial cross so that there are four triangular pouches between the dorsal wall and the stomach. The gonads are situated on the proximal two thirds of the radial canals. There are four radial canals and four long, wavy gonads. Each tentacle bulb has a short core of endodermal cells which extend into the mesogloea.

Marginal vesicles alternate with tentacles, there being ten to twelve tentacles per quadrant.

Diagnosis. This is the first record of this genus in Atlantic waters. It most closely resembles *Halistaera brunii* Navas 1969 from the Bay of Bengal, except that *H. n. sp.* has long wavy gonads. The third member of this genus, *Halistaera cellularia* (L. Agassiz 1865) differs from the new species by having 250-300 tentacles with only 16 to 24 marginal vesicles. The morphology of the three species of *Halistaera* is summarized in Table 15.

*Eucheilota* n. sp.  
Figure 19

Material. Table 16.

Description. The bell is 4 mm in diameter, has a thin jelly and is slightly subhemispherical. There are four perradial tentacles, each flanked by four pairs of lateral cirri. There are no

TABLE 15  
MORPHOLOGIC SUMMARY OF THE THREE KNOWN SPECIES OF Haliastora

	Gonads	Stomach & mouth lips	Marginal vessicles	Marginal tentacles
<u>H. cellularia</u>	long, narrow	small, wavy lips	16-24	250-340
<u>H. brunii</u>	short & spindle shaped	average size slightly un- dulated lips	40-70	40-70
<u>H. n. sp.</u>	long & wavy	short, crenulated	40-48	40-48

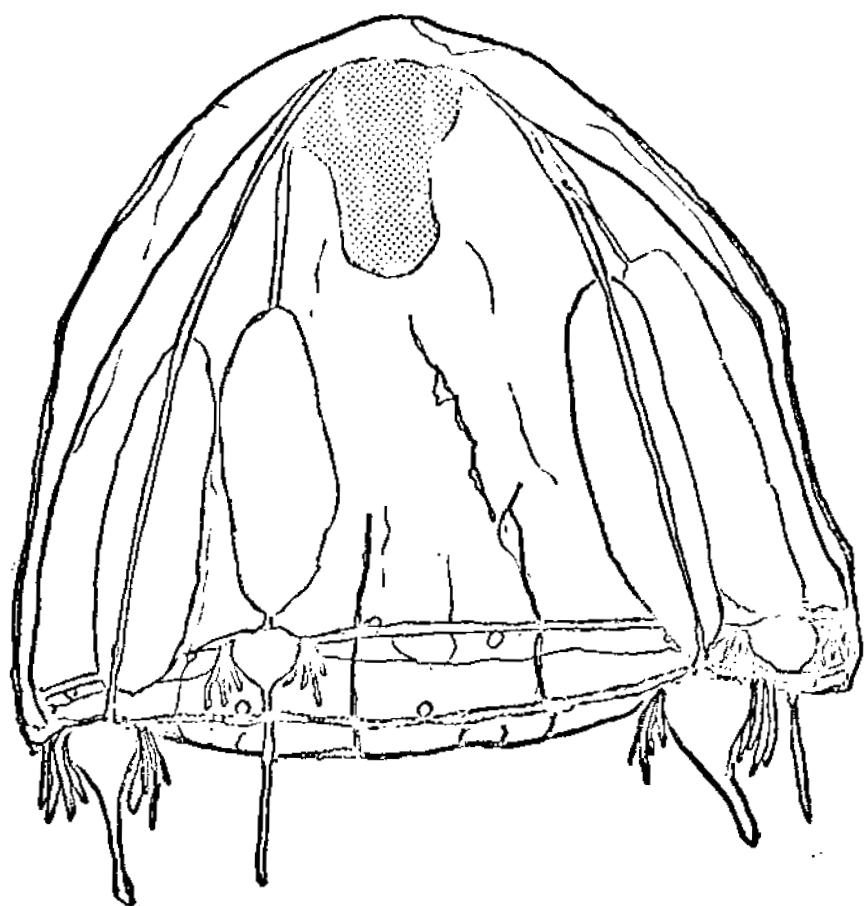


Figure 19. Fuchellota n. sp. Bell diameter is 4 mm.

TABLE 16  
COLLECTION DATA FOR Eucheilota n. sp. TAKEN IN THE NERITIC NORTHERN GULF

Station	Surface* Temperature (C)	Surface** Salinity (o/oo)	Number Taken	Bell Diameter (mm)
6-10-68	4	32.0 (26.4)	36.6 (36.7)	1 2.0
8-14-68	1	29.0 (29.0)	29.9 (29.8)	1 2.0
9-25-68	6	27.0 (18.9)	35.7 (37.4)	1 2.5
10-23-68	2	25.0 (24.8)	36.0 (35.7)	1 2.0
12-9-68	2	16.2 (16.3)	33.2 (33.2)	1 2.0
1-22-69	3	17.0 (15.4)	34.9 (35.7)	2 4.0 3.5
1-23-69	4	14.7 (14.0)	32.6 (33.8)	6 2.5 2.0 2.5 2.5 3.0 3.5
<u>Total Number = 13 Mean = 2.6</u>				

\*Midwater temperature in brackets ( ).

\*\*Midwater salinity in brackets ( ).

rudimentary marginal bulbs. Twelve closed marginal vesicles are present, each containing one to three concretions. Gonads are spindle-shaped and located on the distal two thirds of the radial canals. The velum is well developed. The stomach is short and quadratic with four simple lips.

Diagnosis. This species most closely resembles Eucheilota duodecimalis A. Agassiz 1862; however, E. duodecimalis has only one pair of lateral cirri per tentacle and has only one concretion per marginal vesicle. Pertinent ecological and morphological data for this species are given in Table 16.

Octophialucium n. sp.  
Figure 20

Material. Table 17.

Description. The bell diameter is 13 mm and the jelly is two to three mm thick. The bell is subhemispherical. There are seven very narrow radial canals and 30 short marginal tentacles with broad basal bulbs. Excretory papillae are present. There are up to three closed marginal vesicles, each with up to four concretions, between successive tentacles. There are also one to four immature marginal bulbs between successive tentacles. The mouth is small and quadratic with four simple lips. Gonads are spindle-shaped and located on the distal one fifth of each radial canal.

Diagnosis. Kramp (1959) reported Octophialucium sp. from the western Atlantic; Kramp's specimens, however, were in very poor shape, thus preventing a specific determination. The four mouth

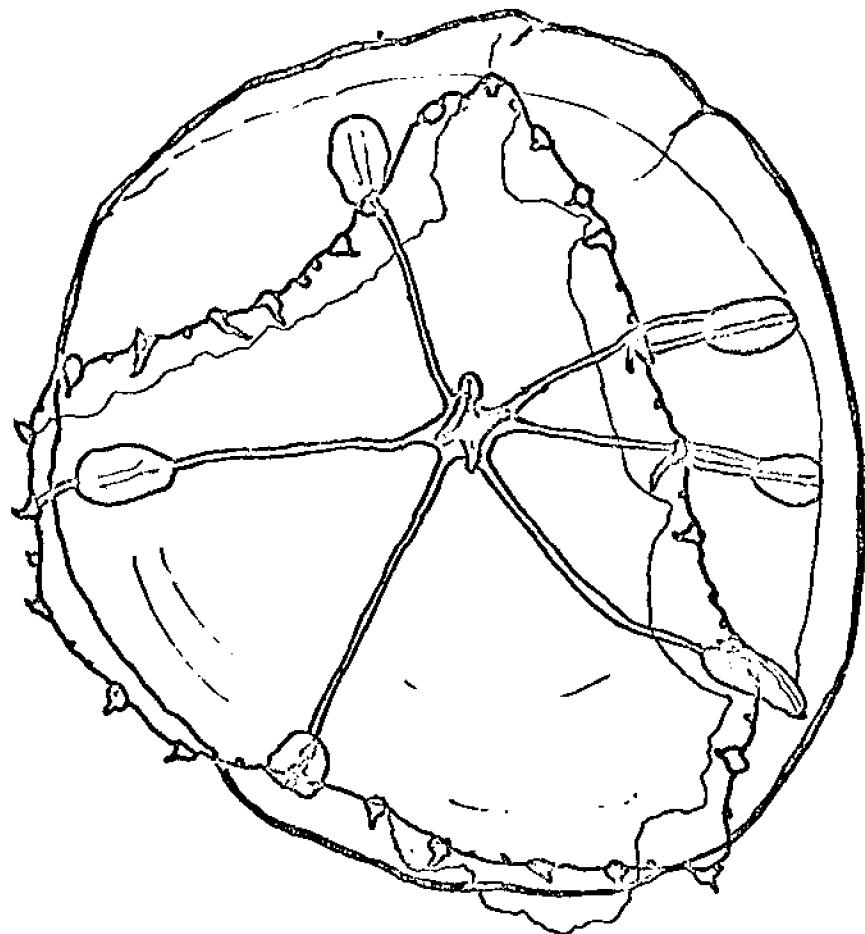


Figure 20. *Octophialucium n. sp.* Bell diameter is 7 mm.

lips distinguish this species from all other described members of the genus which have eight mouth lips. Although the radial canal number is variable in the newly described species (five to eight), the usual number appears to be eight. The morphology of the present specimens and ecological collection data are given in Table 17. From the limited data available it appears that there is an increase in tentacle number with bell diameter along with a decrease in the number of immature tentacle bulbs. There is probably an increase in the number of statocysts with growth; however, this is difficult to evaluate because of the poor condition of the bell margin in three of the specimens. The three specimens having gonads are female, having approximately 16 ova per gonad.

Ecology. *Octonhialicum* n. sp. is a high salinity northern Gulf neritic species (see Table 17). The one specimen taken inside Mississippi Sound off the north beach of Horn Island, was probably due to an influx of neritic water through the island pass into the estuary.

*Benthotriara depressa* Naumov 1960  
Figure 21

Remarks. This Pacific medusa was previously reported only from the Sea of Okhotsk, Kurile Islands and the Bering Sea. The occurrence of this form in tropical western Atlantic waters is indeed a enormous range extension. The present specimen is in excellent condition and there can be no doubt as to its identification despite its small size. The present specimen is 7.5 mm high, and

TABLE 17  
DISTINCTIONAL AND MORPHOMETRIC DATA FOR *Octobrachium n. sp.*  
IN NORTHERN GULF NEAR THE ANDES

Date	Station	Salinity (Surface)	Water Temp. (Surface)	Bell Diameter (mm)	No. of Radial Canals	Gonad No. & Condition	No. of Tentacles	No. of tentacles between bulbs	No. of successive tentacles	No. of tentacles
10-27-67	2 (offshore)	34.5	22.5	13.0	5 (probably 6)	5, female	20*	?	?	1-3
6-18-68	2 (offshore)	31.6	25.5	6.0	8	8, female	12	3-4	2-3	
8-7-68	13 (inshore)	28.3	30.9	7.0	8	8, female	11+	3-4	2-3	
9-24-68	3 (offshore)	35.7	28.5	7.0	6	absent	30	0-1	1-2	
	3 (offshore)			3.0	7	absent	10	1-2	2-3	

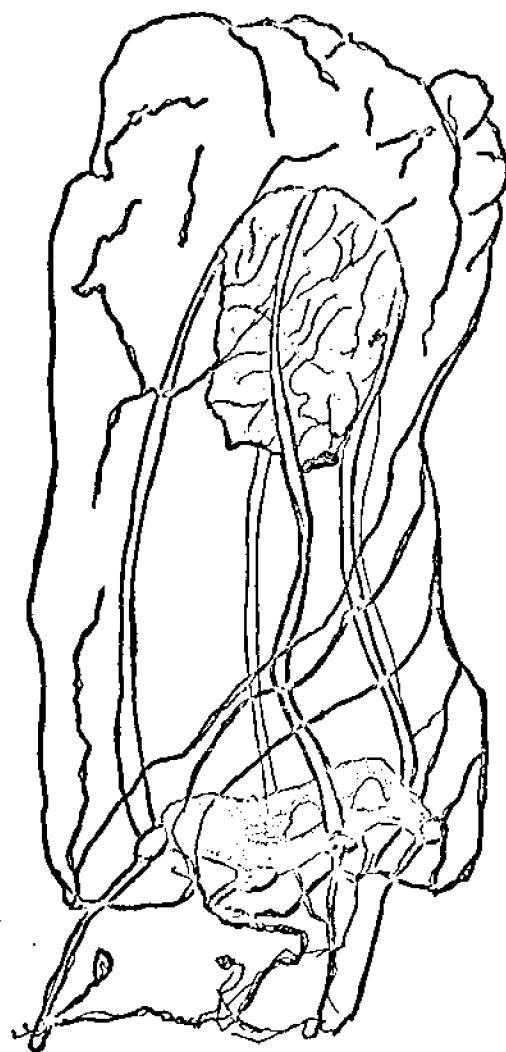


Figure 21. *Bythotifera depressa*. Bell height is 7.5 mm.

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4.0 mm in diameter. The stomach is 2.4 mm in length and there are only seven tentacle bulbs (4 periradial and 3 interradial) as opposed to the normal condition of 8 tentacle bulbs. The North Pacific specimens described by Naumov (1960) are much larger (20 mm height). I do not consider the difference in size or geographic isolation sufficient criteria for erecting a Gulf of Mexico species or subspecies, especially on the basis of a single specimen. B. depressa is easily distinguished from the other two species of Bythotilara by the folded gonads (Figure 21) which cover almost the entire length of the manubrium.

Calyconsis simulans (Bigelow 1909)  
Figures 22 and 23

Material. R/V ALAMINOS: Collection 1, two specimens  
Collection 7, two specimens  
Collection 12, two specimens

Distribution. This is the first record of this form in the Atlantic Ocean. Kramp (1968) lists its Pacific distribution as follows: Indian Ocean; Mombasa, East Africa; Philippines; the Gulf of Panama. Kramp (1968) lists this form as a slope species of intermediate depth "neither neritic nor oceanic, mainly occurring in the deeper water layers, but presumably meropelagic, being derived from hydroids attached to the bottom of continental slopes outside the neritic areas." As Kramp (1968) points out their distribution cannot be explained by ocean currents. Evidently the occurrence of this species in the western Atlantic is evidence of a previous faunal continuity between what are now Atlantic

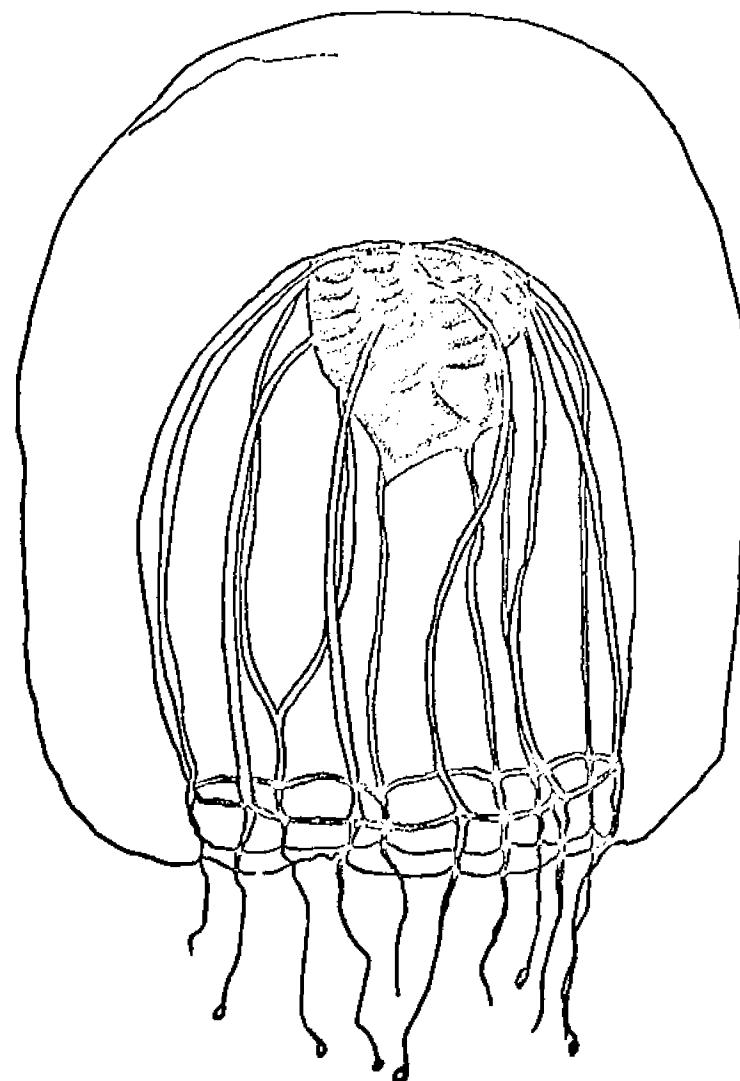


Figure 22. *Calycozois simulating*, adult. Bell height is 18.5 mm.  
Note the presence of 5 centripetal canals, one of  
which is branched near its origin.

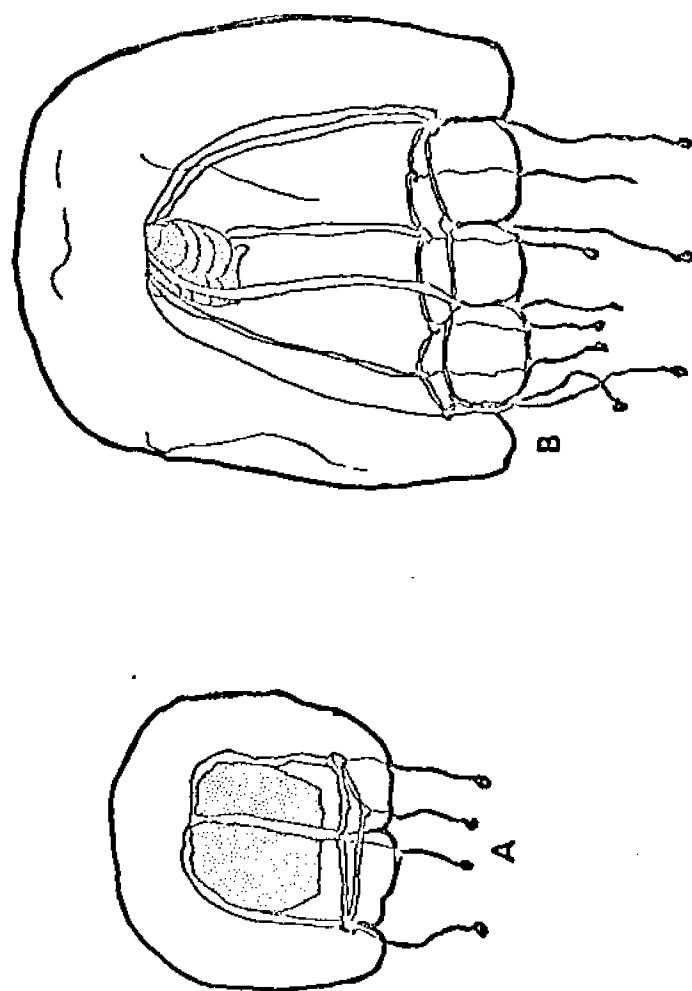


Figure 23. *Calycoensis simulans*, two juveniles. A is 3 mm in bell height and B is 8 mm in bell height. Note absence of centripetal canals.

and Pacific tropical waters. Kramp (1968) states that deepwater shelf species such as Calycopsis sirolans have a very scattered distribution in Indo-Pacific waters and "no reliable zoogeographical conclusions can be drawn from their occurrence," at least with respect to Pacific distributions. The occurrence of this form in the Gulf of Panama and the Gulf of Mexico, two areas separated by a very narrow isthmus, certainly indicates that the Atlantic population most probably had an eastern Pacific origin.

Morphology. Morphologically the present specimens are peculiar in several respects. Kramp (1959) describes a significant difference between South American specimens and a Philippine specimen. The South American specimens have no more than twelve tentacles and all of the centripetal canals are blind, in contrast to the greater number of tentacles (16) and seven of eight centripetal canals connected to the manubrium in the smaller Philippine specimen. Morphologically (Table 18, Figures 22 and 23) the Gulf of Mexico-Yucatan Basin specimens, when mature, have a maximum of twelve tentacles and possess only blind centripetal canals. The centripetal canals in the present specimens develop when the medusa reaches about 8 mm in bell height. Increase in tentacle number and canal number probably occurs as a function of bell growth. The present specimens resemble the Colombian specimens mentioned by Kramp (1959) wherein the gonads are a "pale ochre" in color. These data definitely indicate a previous, probably Pliocene, continuity with the South American population.

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TABLE 18  
MORPHOLOGIC DATA FOR GULF OF MEXICO SPECIMENS OF *Calycopsis simulans*

Collection	Bell Height (mm)	Bell Diameter (mm)	Tentacle Number	Number of Centripetal Canals
1	4.0	4.0	12	8
	5.0	5.0	12	9
7	8.0	5.0	9	absent
	3.0	3.0	4	absent
12	18.5	18.0	11	7*
	10.5	10.0	12	8

\*As shown in Figure 23 one of the centripetal canals branches near its point of origin into two long branches.

Kramp (1959), in his discussion of speciation of Calycopsis, states that C. simulans "is the only species which occurs in the tropical Pacific, in the eastern as well as in the western parts, and apparently certain differences have arisen in the two widely separated populations." From the present information we will have to consider the South American and Gulf of Mexico specimens to constitute a subspecies of C. simulans.

Bougainvillia carolinensis (McCrady 1857)

Remarks. This is an extremely common medusa in northern Gulf waters during Spring and summer months. Its occurrence is discussed in the section on ecology and seasonal occurrence of northern Gulf medusae. There are at least two well defined populations of this form in the northern Gulf. The comparative morphology of these forms is discussed in greater detail following the account of this family. A small juvenile (2 mm height) and an adult are shown in Figures 40-42. Kramp (1959) gives the distribution of this form, reported from Woods Hole to Florida and in the Gulf of Guinea. This is the first report of the medusa from the Gulf of Mexico. The hydroid stage has previously been reported from Louisiana and Florida (cf. Defenbaugh 1970 for distribution in Gulf).

Bougainvillia frondosa Mayer 1900

Remarks. This is a rare neritic species in northern Gulf waters, encountered only on four occasions. It is distinguished from

B. carolinensis by its small size (2 mm high), by having only two tentacles per tentacle bulb and by the complete absence of ocelli. This form has been previously reported from the Dry Tortugas (Mayer 1900, 1910), this being the first report from the northern Gulf. Evidently B. frondosa may be considered endemic to the West Indian-Gulf of Mexico faunal region.

Bougainvillia polygaster (Haeckel 1879)

Material. R/V ALAMINOS: Collection 2, 12 specimens  
Collection 8, 1 specimen  
Collection 14, 1 specimen  
Collection 18, 1 specimen

Remarks. This species is very common in southern Gulf waters and the Yucatan basin. Kramp (1957) compared B. platygaster, B. carolinensis, B. fulva, and B. niebe and concluded that the four species are distinct. The development of medusa buds on pedicels of typical hydranths has been discussed by Kramp (1959, 1957). Almost all the present specimens, including those parasitized by narcomedusan larvae, exhibited this asexual budding at the corners of the stomach. Obviously, this form may be holoplanktonic, bypassing a sessile hydroid stage. The present medusae are most probably epiplanktonic, since the largest number were taken in upper water strata by a meter net (Collection 2).

Bell diameter of present specimens ranged from 4 to 8 mm. Bell diameter and number of tentacles per tentacle bulb are given in Table 19.

TABLE 19  
BELL DIAMETER AND NUMBER OF TENTACLES PER MARGINAL BULB FOR  
GULF OF MEXICO Bougainvillia platygastra TAKEN BY R/V ALAMINOS

Collection	Diameter	Tentacles per Bulb
2	8.0	14
	7.0	11
	7.0	12
	6.0	13
	7.0	12
	7.5	14
	4.0	10
	6.0	11
	52.5	97
Mean =	6.6	12.1

Distribution. This medusa has previously been reported off the east coast of Brazil, and has been reported from several localities in West Indian waters by Kramp (1959). It is also found in the Canary Islands, Cape Verde Islands and off the east coast of Africa.

Nemopsis bachei L. Agassiz 1849

Remarks. This is an extremely common winter and spring medusa in northern Gulf waters. Its distribution and ecology are discussed in the section dealing with seasonal occurrence of medusae in northern Gulf waters and its morphology is discussed and compared with B. carolinensis in the next section. This medusa is easily distinguished from all other Gulf bougainvilliids by the radial lobes of the stomach which extend outward onto the radial canals up to one half to two thirds the length of the radial canals. The

significance of this species in northern Gulf estuarine food webs has been discussed by Phillips et al. (1969).

Koellikerina n. sp.  
Figure 24

Material. R/V ALAMINOS: Collection 12, twelve specimens

Diagnosis. Size ranges from 4 to 10 mm in bell height and diameter, which are equal. The peduncle is short and broad (up to 5 mm) and the oral tentacles are divided in excess of eight times. The gonads are periradial, horseshoe-shaped, orange in color, and each have two rows of five transverse folds. There are 16-27 tentacles each with an adaxial ocellus per each of the eight marginal tentacle bulbs. Pertinent measurements regarding bell dimensions and tentacles per tentacle bulb are given in Table 20. This species most closely resembles the eastern Atlantic Koellikerina fasciculata which according to Kramp (1961) is found in the Black Sea and Mediterranean. K. fasciculata, however, has only 10-13 tentacles in each of the marginal clusters and its oral tentacles branch only up to seven times.

Discussion. The present form is obviously closely related to the east Atlantic fasciculata since the only distinguishing feature is relative number of tentacles. This species brings the total number of species in this genus to eight, four of which are Pacific only, and one Antarctic. The only other Atlantic form, K. elegans (Mayer 1900), known from Dry Tortugas, has a wide Indo-Pacific distribution. It seems quite probable that the Atlantic K. n. sp.

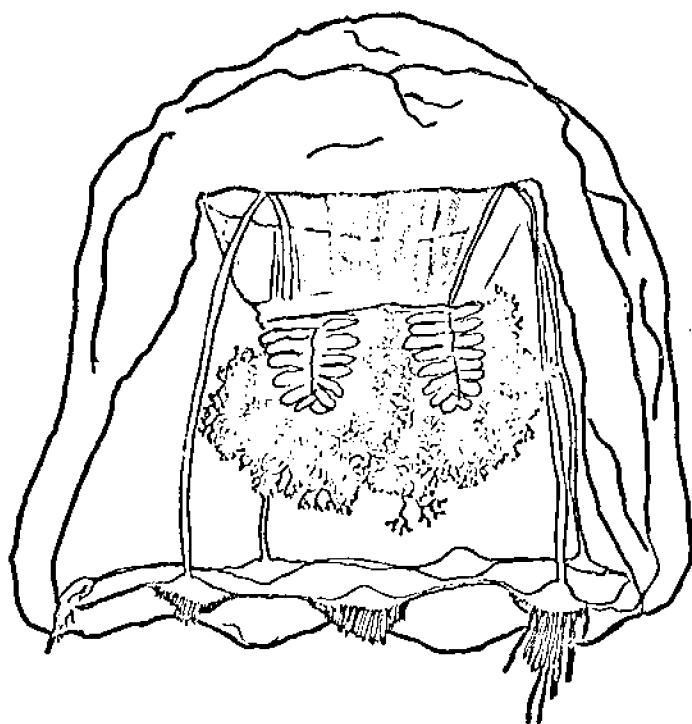


Figure 24. Koellikerina n. sp. Bell diameter is 10 mm.

TABLE 20  
BELL MEASUREMENTS AND PERTINENT REPRODUCTIVE DATA FOR  
*Kochlikerina* n.sp.

	Height (mm)	Bell Diameter (mm)	<u>Tentacles per Bulb</u>	
			Perradial	Interradial
Molotype	10	10	23,27	26
<b>Paratypes</b>				
1	9	9	23	22
2	9	9	22	22
3	7	6	16	not determined
4	8	8	damaged	damaged
5	8	8	16	16
6	7	8	18	18
7	7	9	18	18
8	7	7	16	16
9	7	7	20	22
10	7.5	7.5	20	20
11	8	8	20	18
12	4	4	18	18
$\Sigma$	9.5	101.0	231	220
mean	7.6	7.8	19.3	18.4

and K. fasciculata were derived from a single stock which had been split off from Indo-Pacific populations by the emergence of Central America in the Pliocene and that K. elegans invaded the Atlantic at a different time.

Dichotomia cannoidea Brooks 1903

Material. R/V ALAMINOS: Collection 2, 5 specimens  
Collection 3, 6 specimens

Remarks. Although Kramp (1959) lists these medusae as occurring "from the West Indies and the waters north of these islands up to about 39°N" no specimens were taken north of 25° in the present study. Evidently this epipelagic form (taken only in meter nets) is restricted to tropical waters of the Gulf. It is probably carried northward to 39° on the American coast by the Gulf stream. Allwein (1967) does not record this species from North Carolina waters.

The present specimens range from 3 to 5 mm in bell height and in diameter.

Orchistoma pileus (Lesson 1843)

Material. R/V ALAMINOS: Collection 22, 1 specimen  
Collection 5, 3 specimens  
Collection 2, 1 specimen  
Collection 10, 1 specimen  
Collection 3, 9 specimens  
Collection 8, 3 specimens

Remarks. This is a common, epipelagic, tropical form found throughout the West Indian faunal region. Bell diameter varied from 12 to 26 mm in bell diameter. As can be seen from the morphometric

data presented below in Table 21 there is apparently no increase in tentacle or radial canal number with increasing bell diameter.

TABLE 21  
MEASUREMENTS OF Orchistoma pileus OF THE GULF OF MEXICO

<u>R/V ALAMINOS</u>		Number of	
Collection	Bell Diameter	Tentacles	Radial Canals
2	22.0	34	not taken
3	12.0	40	32
	25.0	47	33
	20.0	43	35
	26.0	44	34
	15.0	45	32
	23.0	38	32
	20.0	36	26
	17.0	missing	28
5	25.0	damaged	damaged
	20.0	"	"
	12.0	"	"

Several interesting canal anomalies were observed. These anomalies involve crosslinking, branching fusion and formation of loops. The only other leptomedusan in which a high frequency of canal anomalies was encountered is Eirene pyramidalis.

Zygocanna vagans Bigelow 1912

Material. R/V ALAMINOS: Collection 12, 2 specimens  
Collection 9, 7 specimens

Remarks. This is the first record of this acroreid medusa in the western Atlantic. It has previously been reported from the Philippines, from the Pacific coasts of Panama and Columbia.

from west of the Cape of Good Hope and from the Azores (Kramp 1959).

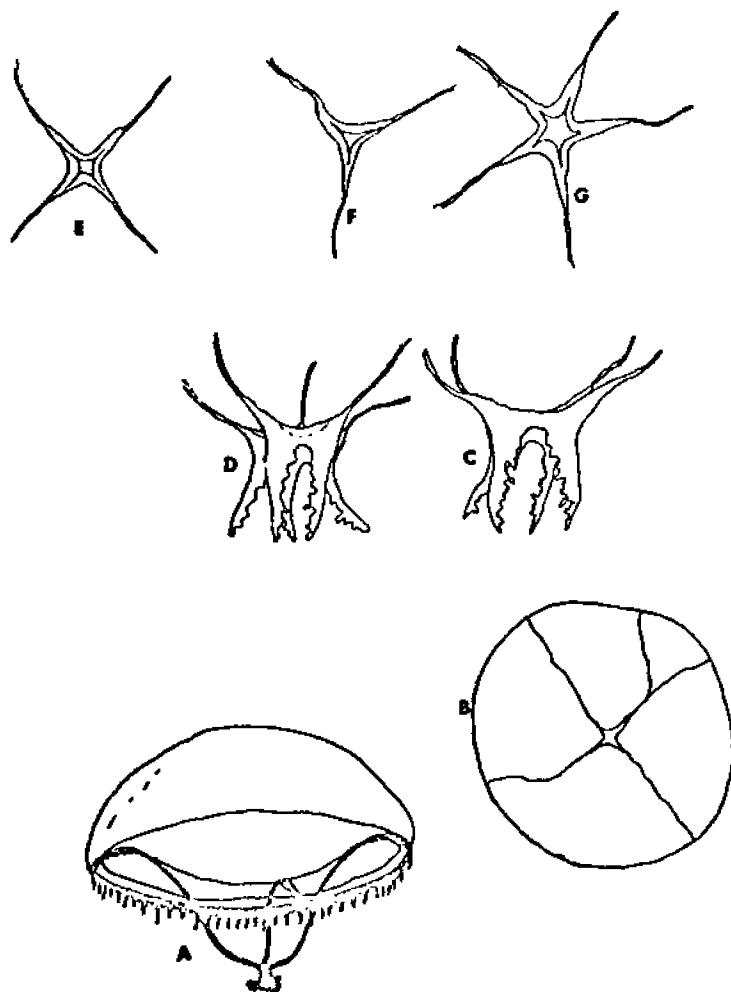
This species is easily recognized by the multiple branching of the radial canals inside the stomach (cf. Kramp 1959, Figure 274) and by the radial rows of gelatinous papillae on the subumbrella.

The present medusae range in size from 20 to 60 mm in diameter.

Eirene pyramidalis (L. Agassiz 1862)  
Figure 25

Remarks. This rather striking leptomedusan occurs in tremendous shoals during summer and fall in northern Gulf waters, often completely filling plankton nets. This species is a typical summer component of the northern Gulf leptomedusan fauna, restricted to relatively shallow offshore waters.

The relationship of bell diameter to tentacle number is shown in Figure 26. The relationship of tentacle number to bell diameter is linear and can be expressed by the regression curve (shown in Figure 26) of  $Y = 25.9262 + 3.0484 X$ , where  $Y$  is the number of tentacles and the correlation coefficient is 0.86. For the 52 specimens measured mean bell diameter is 18.6 mm (s.d.=6.66) and mean tentacle number is 82.7 (s.d.=23.73). About ten percent of the 52 specimens examined exhibited canal anomalies of the types shown in Figure 25 B-G. (The data regarding exact frequency were lost in Hurricane Camille). Some of these anomalies are comparable to those found in Octophialicum and Orchistoma pileus. The number of mouth lips is related to the number of radial canals in a one to one correspondence as can be seen from Figure 25. In



**Figure 25.** *Firenec pyramidalis*: View of adult and canal anomalies. A is lateral view of adult (10 mm diameter); B is exumbrial view of specimen with a branched radial canal; C and D depict normal four-armed manubrium and abnormal five-armed manubrium; E-G are aboral views of four-armed, three-armed and five-armed manubria respectively.

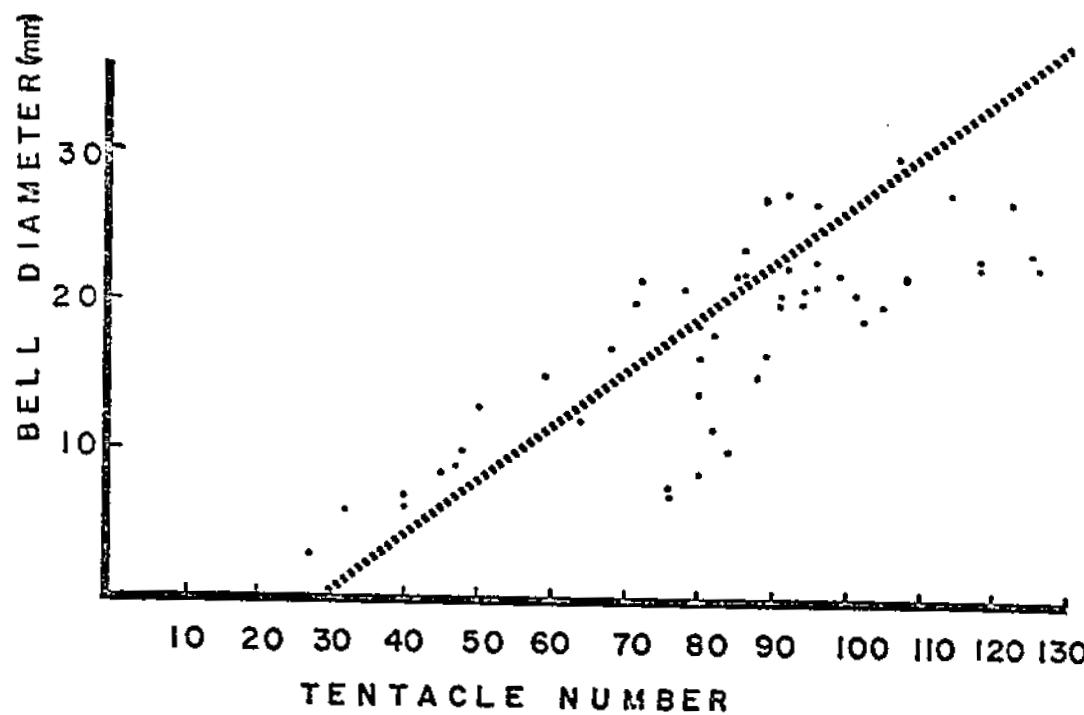


Figure 26. Eirene pyramidalis: Bell diameter vs. tentacle number.

contrast to Orchistoma pileus the tentacle number in E. pyramidalis does not reach a maximum at an early growth stage, but increases linearly with growth of the bell.

Proboscidactyla ornata McCrady 1857  
Figure 27

Remarks. This is a relatively common medusa in all Gulf waters and, according to Kramp (1959), is circumglobal in warm coastal waters. Most of the present specimens bore on the radial canals and gonads, hydroid-like stolons which had attached medusae buds (Figure 37). The hydroid of this form (Lar), which is parasitic or commensal on sabellid worm tubes (Russell 1959), has not been reported for the Gulf. Perhaps this limnomedusan, by virtue of medusa budding, may complete an entire life cycle in the plankton.

Haliscera bigelowi Kramp 1947

Material. R/V ALAMINOS: Collection 18, one specimen at depth between 1600 and 2500 mm

Remarks. The present specimen is 15 mm in diameter. Both the bell margin and endoderm of stomach are a yellowish orange. The occurrence of this and other trachymedusae at this depth is indicative that a well developed bathypelagic cnidarian fauna exists in the Gulf. This species is found in deep waters of the eastern tropical Pacific and the northern Atlantic from south of Iceland to the northwest coast of Africa. This is the first record of this form from the Gulf-West Indian region.

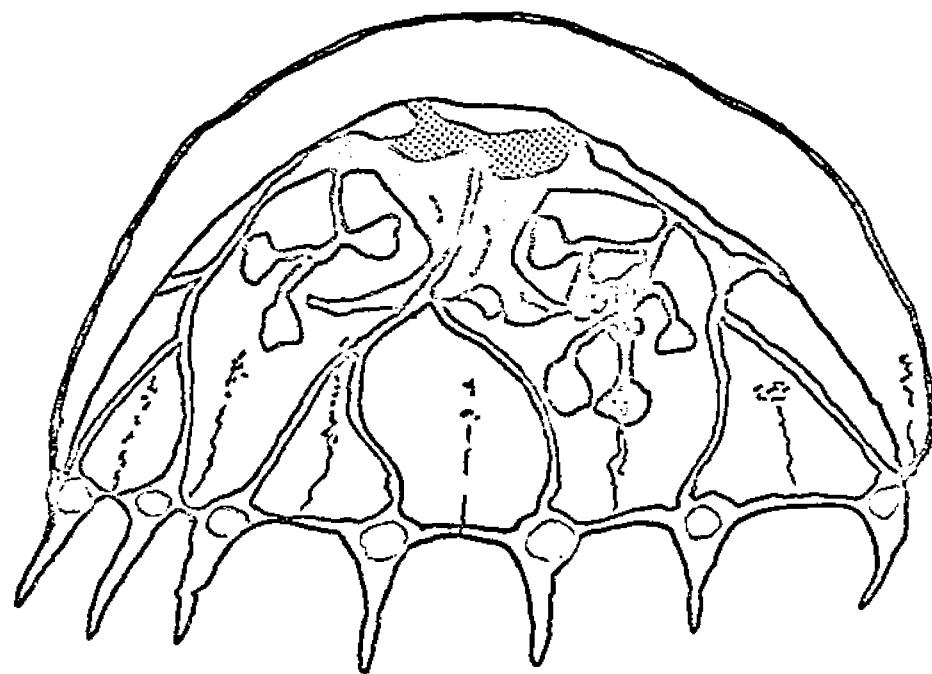


Figure 27. Proboscidactyla ornata. Bell diameter is 6 mm. Note the hydroid-like outgrowths from the radial canals.

Aeginia citrea Eschscholtz 1829

Material. R/V ALAMINOS: Collection 7, 1 specimen (damaged)  
 Collection 18, at depth 1025-1240 m,  
 one specimen

Remarks. The undamaged specimen was taken in intermediate water (1025-1240 m) and had a diameter of 20 mm and 4 tentacles. This medusa has a very wide distribution in warm and temperate waters. The closest previous locality record is that by Mayer (1910) wherein a specimen is recorded from the Bahamas.

Aeginura grimaldi Maas 1904

Material. R/V ALAMINOS: Collection 12, one specimen  
 Collection 18, at depth (1025-1240 m),  
 one specimen

Remarks. This is a widely distributed bathypelagic form. It has not, however, been previously reported from West Indian waters although it occurs near Bermuda. This is the first record for this region of the Atlantic.

Morphometrics of the two specimens are as follows:

	Diameter	Tentacles	Stomach Pouches
Station 12	17	8	16
Station 21	15	13	damaged

The large number of tentacles in the second specimen is due to the development of 5 small secondary tentacles.

Solmundella bitentaculata (Quoy and Gaimard 1833)

Material. R/V ALAMINOS: Collection 12, one specimen

Remarks. This is a very common epipelagic form in all warm and tropical waters. Its occurrence in northern Gulf neritic waters is discussed in the section on the ecology of the northern Gulf medusae.

Pegantha martagon Haeckel 1870  
Figure 28

Material. R/V ALAMINOS: Collection 12, 3 specimens

Remarks. Kramp (1968) gives the following distribution: eastern tropical Pacific (Gulf of Panama), China Sea, tropical Indian Ocean, the Azores, West Indies, east coast of South America and circumpolar in the subantarctic sea.

The present specimens vary from 12 to 60 mm in diameter and have 14-19 tentacles. The large diameter of 60 mm is unusual for this species (Kramp 1968 lists maximum size as 30 mm). The gonads lack diverticula and the festoon canals have broad lateral portions. No sense organs were seen on any specimens which may possibly have been due to abrasion in the collecting device. The lappets are square to rectangular. Parasitic larvae were found in the canals and gonads of the largest specimen only. Pertinent morphometrics for the three specimens are as follows:

Diameter	Number of tentacles
60	14
25	15 + (bell damaged, at least 1 tentacle missing)
12	19

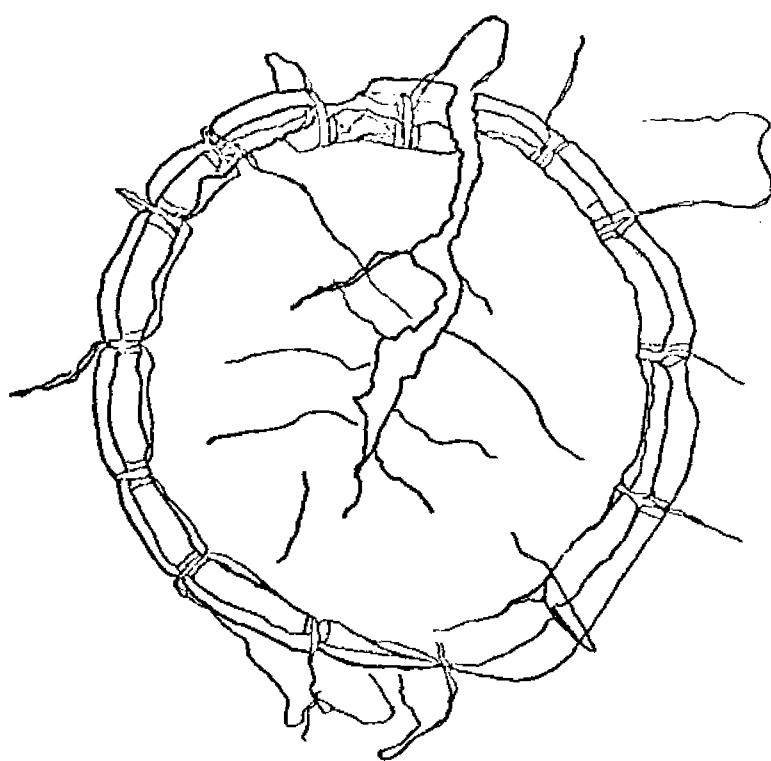


Figure 28. *Pegantha martagon*. Bell diameter is 60 mm. In this oral view the stomach pouches (stippled areas) are clearly visible.

From the limited data it is apparent that the growth pattern in Gulf of Mexico *P. martagon* is identical with that given by Kramp (1957, 1959a) for other populations wherein each specimen usually attains its maximum number in early development.

Cunina octonaria McCrady 1857

Material. R/V GERONIMO: Collection 16-17 (see Figure 4)

Remarks. This is the commonest species of Cunina in northern Gulf waters, occasionally occurring in large blooms. It is evidently epipelagic. This species is found in warm waters of all oceans.

Cunina fowleri (Browne 1966)

Material. R/V ALAMINOS: Collection 1, 1 specimen  
Collection 3, 1 specimen

Remarks. Two specimens, 4 and 5 mm diameters respectively, were taken in S. E. Gulf waters. The 4 mm specimen had numerous medusae buds developing from the stomach pouches. The only previous record is from the Bay of Biscay. Apparently this species is endemic to the South Florida-Gulf region. The present specimens were taken in the upper 100 m indicating this is an epipelagic form.

Cunina duplicata Mnas 1893

Material. R/V ALAMINOS: Collection 12, 2 specimens

Remarks. The locality from which the two specimens were taken is the northeast Gulf. Kramp (1959) gives its distribution as being central and southern Atlantic, having been reported from the east coast of South America and west coast of Africa. Pertinent

morphometrics of the present specimens are given below:

<u>Diameter</u>	<u>Tentacles</u>	<u>Stomach Pouches</u>	<u>Mouth Opening</u>	<u>Octopores</u>
28	18	18	12	2 on one lappet
12	11	11	3-5	not noted

Apparently, judging from the present data and those presented by Kramp (1959), tentacle number and number of stomach pouches increase linearly with growth. The uneven size of tentacles and stomach pouches in the present specimens may be indicative of this.

Cunina peregrina Bigelow 1909

Material. R/V ALAMINOS: Collection 1, 1 specimen

Remarks. This form is common in northern Gulf waters though not nearly as abundant as C. octonaria. The one specimen collected by the R/V ALAMINOS in the S. E. portion of the Gulf was 5-6 mm in diameter and had 12 stomach pouches and tentacles. This is a very common form in tropical Atlantic, Pacific and Indian Ocean waters.

Solmissus incissa (Fewkes 1886)

Material. R/V ALAMINOS: Collection 4, fragments  
Collection 12, fragmented specimen

Remarks. The fragments taken can be only provisionally identified as S. incissa. The specimen taken at Station 12 appears to have had a diameter of 70-80 mm and 28+ tentacles. Most of the central disk was missing.

Intra- and Interspecific Morphologic Variation in Northern Gulf  
Bougainvilliid Medusae

To date there have been very few quantitative studies of medusa morphology other than a listing of a series of measurements with a numerical mean for characters of systematic or developmental significance. Intraspecific variation studies were attempted by Vanucci (1966) but were abandoned by her because of their considerable tediousness and difficulty, especially with respect to trachymedusae. As previously indicated several forms common in northern Gulf waters appear to differ morphologically and ecologically from populations of the same species in other regions of the Atlantic coast of North America. This is particularly true with respect to the winter jellyfish, Cyanea capillata versicolor, which is geographically isolated in Gulf of Mexico waters from other North Atlantic subspecies. Additionally sea nettles, Chrysaora quinquecirrha, of the Gulf have different ecologic and developmental patterns than populations from Chesapeake Bay (Phillips *et al.* 1969), reaching sexual maturity much earlier and not obtaining the larger size characteristic of Chesapeake Bay medusae. Aurelia aurita has different strobilation patterns in Texas waters as compared with New England coastal regions (Spangenberg, personal communication). In the northern areas strobilation is cold dependent in that the polyps must be exposed to temperatures of 4 C to strobilate. The converse is true with respect to Texas coast forms which require high temperatures (about 16 C) for induction of strobilation.

Although Sanders and Sanders (1963) have erected a Gulf subspecies of the holoplanktonic semaeostome Pelagia noctiluca, calling it P. n. mexicana, I doubt the validity of this subspecific designation. As stated earlier the major reason for not considering it a valid subspecies is that when examining type material at the USNM I could not in any way distinguish the P. n. mexicana specimens from those taken in other tropical waters.

In the case of the anthomedusan Bougainvillia carolinensis, although medusae from different areas may appear homogenous with respect to morphology, differences can be demonstrated in large series of specimens from two different habitats in northern Gulf waters. These two populations include Mississippi Sound and adjacent neritic waters.

Two populations of Bougainvillia carolinensis from Mississippi coastal waters, taken in 1967 and 1968, were compared with respect to oral tentacle branching, bell height, bell diameter, bell cavity height, number of ocelli and number of tentacles per tentacle bulb. Only relaxed undistorted specimens were used. Number of specimens examined from each population varied from 35 to 116. Correlation coefficients were computed for each of the populations for bell height versus bell diameter, bell height versus number of tentacles per bulb, bell height versus number of ocelli per bulb, as well as bell height versus number of oral tentacle branches. B. carolinensis is illustrated in Figures 29-31. Additionally correlation coefficients and regression curves were computed for

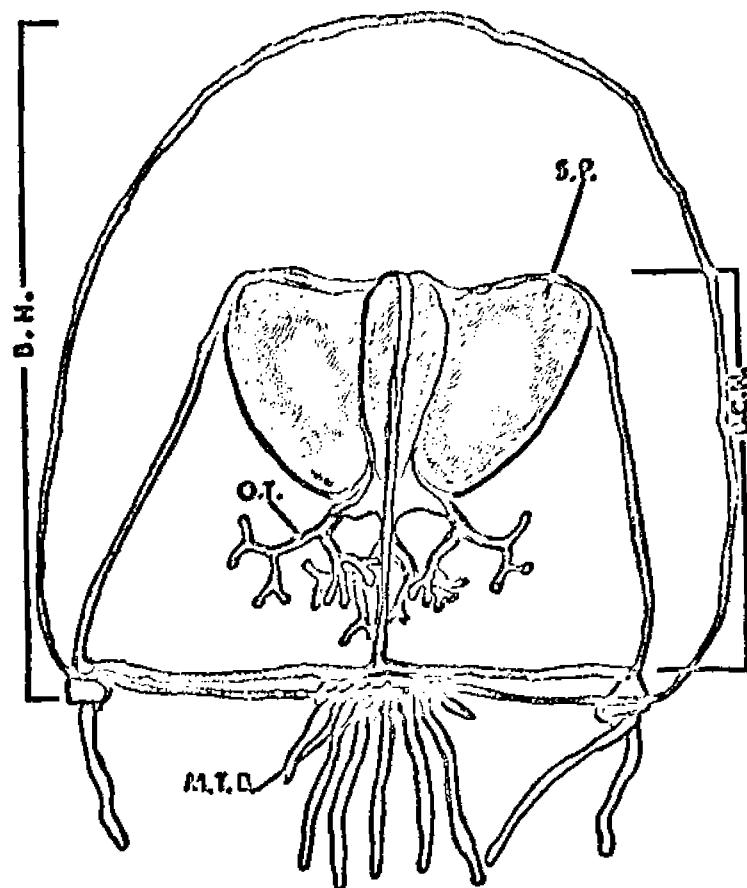


Figure 29. *Bougainvillia carolinensis*, lateral view. Bell height is 5 mm. B.H. indicates bell height; B.C.H. indicates bell cavity height; M.T.B. indicates marginal tentacle bulb; O.T. indicates oral tentacle; S.P. indicates stomach pouch.

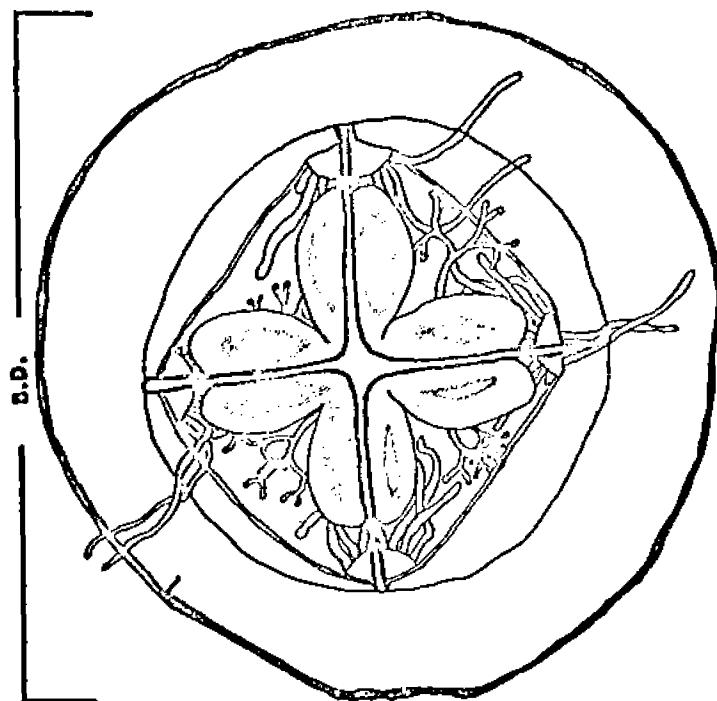


Figure 30. Bougainvillia carolinensis, aboral view. B.D.  
indicates bell diameter.

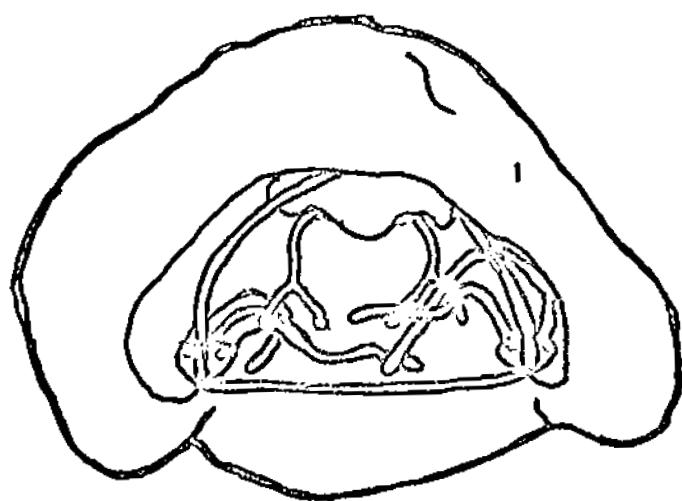


Figure 31. *Bougainvillia carolinensis*, juvenile. Bell diameter is 2 mm. Note that there are only two ocelli and two tentacles on each marginal tentacle bulb and that the oral tentacles have only branched once.

the pooled populations for comparison with growth patterns in Nemopsis bachei, for which identical parameters were evaluated in like manner. Only 23 to 35 specimens of N. bachei were utilized for quantification. In comparing correlation coefficients and regression patterns of the different populations a corrected F value was utilized to correct for possible absolute differences in size. Unadjusted F values are used to compare absolute variances and means.

With respect to all populations of Bougainvillia and Nemopsis considered there are valid positive correlations between the following parameters: (1) bell height and bell diameter; (2) bell height and bell cavity height; (3) bell diameter and bell cavity height. T values, correlation coefficients and other pertinent statistics for the individual populations are given in Tables 22 and 23. As can be seen from the latter table there are significant (at 5% level) correlations between bell height and number of tentacles per bulb, bell diameter and number of tentacles per bulb, and bell height plotted against number of oral tentacle branches for offshore specimens of Bougainvillia carolinensis. No such correlations could be demonstrated for estuarine populations. Data regarding the number of ocelli are not used in this comparison since the delicate nature of these structures and their loss on fixation and preservation causes this parameter to be inaccurate. Ideally there should be identical numbers of ocelli and marginal tentacles or tentacle primordia. These data, given in Table 22 for the two

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TABLE 22  
STATISTICAL COMPARISON OF ESTUARINE AND NERITIC POPULATIONS  
OF Bougainvillia carolinensis IN NORTHERN GULF OF MEXICO WATERS

(Mississippi Sound population is designated as GP 1 and the neritic population designated GP 2. N indicates sample size; DF indicates degrees of freedom; alpha ( $\alpha$ ) indicates significance level. Adjusted means for the second variable are indicated by parentheses. Regression curves are given in the form  $Y=a + bX$ . Variable is abbreviated "var." BH=bell height; BD=bell diameter.)

Variables	GP	Means			F values		
		Var. 1	Var. 2	(Var. 2)	Var. 1	Var. 2	Adjusted Var. 2
BH	1	3.48 Y=0.7	3.49 + 0.8X	(3.31)	23.79 $\alpha$ 0.01	7.23 $\alpha$ 0.01	4.86 DF=192
vs. Diameter							
GP1 N=138							
GP2 N= 56	2	2.72 Y=0.4	3.07 + 0.97X	(3.52)			DF=191
BH	1	3.30 Y=0.1	1.59 X 0.5X	(1.54)	2.51 $\alpha$ 0.01	1.33 $\alpha$ 0.05	15.4 DF=190
vs. Bell Cavity Height							
GP1 N=100							
GP2 N= 92	2	3.1 Y=0.4	1.69 + 0.4	(1.72)			DF=189

TABLE 22 (Continued)  
 STATISTICAL COMPARISON OF ESTUARINE AND NERITIC POPULATIONS  
 OF Bougainvillia carolinensis IN NORTHERN GULF OF MEXICO WATERS

(Mississippi Sound population is designated as GP 1 and the neritic population designated GP 2.  
 N indicates sample size; DF indicates degrees of freedom; alpha ( $\alpha$ ) indicates significance level.  
 Adjusted means for the second variable are indicated by parentheses. Regression curves are given  
 in the form  $Y=a + bX$ . Variable is abbreviated "var." BH=bell height; BD=bell diameter.)

Variables	GP	Means			F values		
		Var. 1	Var. 2	(Var. 2)	Var. 1	Var. 2	Adjusted Var. 2
BH vs. Tentacle No./Bulb GP1 N=105 GP2 N=100	1	3.475 Y=5.9	6.057 + 0.06X	(6.00)	11.46 $\alpha$ 0.01 DF=203	9.52 $\alpha$ 0.01	12.13 $\alpha$ 0.01 DF=202
	2	3.02 Y=4.6	6.81 + 0.6	(6.869)			
BH vs. Ocelli No./ Bulb GP1 N=116 GP2 N= 96	1	3.53 Y=5.2	5.729 + 0.15	(6.56)	9.37 $\alpha$ 0.01 DF=211	16.4 $\alpha$ 0.01	16.3 $\alpha$ 0.01 DF=210
	2	3.109 Y=5.6	6.659 + 0.313X	(6.705)			

TABLE 22 (Continued)  
 STATISTICAL COMPARISON OF ESTUARINE AND NERITIC POPULATIONS  
OF *Bourainvillia carolinensis* IN NORTHERN GULF OF MEXICO WATERS

(Mississippi Sound population is designated as GP 1 and the neritic population designated GP 2. N indicates sample size; DF indicates degrees of freedom; alpha ( $\alpha$ ) indicates significance level. Adjusted means for the second variable are indicated by parentheses. Regression curves are given in the form  $Y=a + bX$ . Variable is abbreviated "var." BH=bell height; BD=bell diameter.)

Variables	GP	Means		F values			
		Var. 1	Var. 2 (Var. 2)	Var. 1	Var. 2	Adjusted Var. 2	
BH vs. No. Oral Tentacle Branches GP1 N=116 GP2 N= 96	1	3.53 $Y=6.1$	6.95 $+ 0.072X$	(6.85) $\alpha < 0.01$ DF=210	13.8 $\alpha < 0.01$	16.2 $\alpha < 0.01$	17.6 $\alpha < 0.01$ DF=209
	2	3.04 $Y=6.1$	10.07 $+ 1.3X$	(10.2)			
BD vs. Tentacle No./Bulb GP1 N=108 GP2 N= 57	1	3.49 $Y=5.9$	6.10 $+ 0.04X$	(6.05) $\alpha < 0.01$	8.7 $\alpha < 0.01$	4.08 $\alpha < 0.01$	5.70 $\alpha < 0.01$
	2	2.99 $Y=4.45$	6.73 $+ 0.75X$	(4.08)			

TABLE 23  
CORRELATION COEFFICIENTS AND REGRESSION EQUATIONS FOR Nemopsis bachei  
AND THE TWO POPULATIONS OF Bougainvillia carolinensis

(B.H.=bell height; B.D.=bell diameter; B.C.H.=bell cavity height; N=sample size; S.D.=standard deviation; S.E.=standard error. The S.E. of the coefficient "b" of the equation  $Y=a+bX$  is given in parentheses under the equation.)

Variables	N	Mean of X	S.D. X	S.D. Y	Correlation Coefficient and Regression Equation	T
<u><i>Nemopsis bachei</i></u>						
B.H. vs. B.D.	35	6.01	1.56	2.44	0.87; $Y=-1.1+1.4X$ (0.13)	10.1
B.H. vs. B.C.H.	13	5.05	1.33	1.08	9.05; $Y=-0.3+0.8X$ (0.08)	10.0
B.H. vs. No. Tentacles/Bulb	34	6.02	1.58	5.36	0.61; $Y=6.1+1.21X$ (0.47)	4.4
B.H. vs. No. Oral Tentacles Branches	23	6.05	1.84	7.86	0.24; $Y=15.3+1.1X$ (0.91)	1.1
B.D. vs. No. Tentacles/Bulb	35	7.18	2.50	5.51	0.68; $Y=8.1-1.5X$ (0.28)	5.4

TABLE 23 (Continued)  
 CORRELATION COEFFICIENTS AND REGRESSION EQUATIONS FOR Nemopsis bachei  
 AND THE TWO POPULATIONS OF Bougainvillia carolinensis

(B.H.=height; B.D.=bell diameter; B.C.H.=bell cavity height; N=sample size; S.D.=standard deviation; S.E.=standard error. The S.E. of the coefficient "b" of the equation  $Y=a + bX$  is given in parentheses under the equation.)

Variables	N	Mean of X	S.D. X	S.D. Y	Correlation Coefficient and Regression Equation	T
<u>Bougainvillia carolinensis:</u> Mississippi Sound Population (GP 1)						
B.H. vs. B.D.	138	3.48	1.04	1.03	0.81; $Y=0.7+0.8X$ (0.04)	16.4
B.H. vs. B.C.H.	100	3.30	0.92	0.57	0.83; $Y=-0.1+0.5X$ (0.04)	14.6
B.H. vs. No. Tentacles/Bulb	105	3.48	1.07	0.03	0.16; $Y=5.9+0.1X$ (0.16)	0.3*
B.H. vs. No. Oral Tentacle Branches	116	3.53	1.04	5.96	0.01; $Y=6.7+0.1X$ (0.54)	0.13*
B.D. vs. No. Tentacles/Bulb	108	3.50	1.05	1.78	0.03; $Y=5.9+0.1X$ (0.16)	0.28*

TABLE 23 (Continued)  
 CORRELATION COEFFICIENTS AND REGRESSION EQUATIONS FOR Nemopsis bachei  
 AND THE TWO POPULATIONS OF Bougainvillia carolinensis

(B.H.=bell height; B.D.=bell diameter; B.C.H.=bell cavity height; N=sample size; S.D.=standard deviation; S.E.=standard error. The S.E. of the coefficient "b" of the equation  $Y=a+bX$  is given in parentheses under the equation.)

Variables	N	Mean of X	S.D. X	S.D. Y	Correlation Coefficient and Regression Equation	T
<u>Bougainvillia carolinensis:</u> Offshore Neritic Population (GP 2)						
B.H. vs. B.D.	56	2.71	0.80	0.91	0.86; $Y=0.4+0.9X$ (0.07)	12.6
B.H. vs. B.C.H.	92	3.11	0.75	0.43	0.73; $Y=0.4+0.4X$ (0.04)	10.2
B.H. vs. No. Tentacles/Bulb	100	3.02	0.79	1.70	0.29; $Y=4.9+0.6X$ (0.20)	3.06
B.H. vs. No. Oral Tentacle Branches	96	3.05	0.80	5.14	0.20; $Y=6.1+1.3X$ (0.65)	2.01
B.D. vs. No. Tentacles/Bulb	57	3.00	0.96	2.15	0.33; $Y=4.5+0.7X$ (0.28)	2.67

\*No significant correlation.

populations of Bougainvillia, indicate that growth patterns are indeed different in individuals of the two populations, the offshore population exhibiting linear increase in marginal tentacle number and branching of oral tentacles. Those differences are further manifest when individual parameters and correlations within populations are compared as in Table 22. As can be seen from Table 22, the linear correlations between gross bell dimensions (height and breadth) are significantly different in the two populations.

Although morphologically so similar on visual inspection, that it is impossible to identify the source of an individual specimen of B. carolinensis with certainty, there are indeed subtle differences in the two different populations. Differences in morphometric patterns are presented graphically in Figure 32. The most striking (Figure 32B) is that of the number of tentacles per tentacle bulb in the estuarine population wherein there is apparently no increase in tentacle number beyond that obtained early in growth, indicating a marked allometric growth pattern that is also exhibited by the number of oral tentacle branches (not shown graphically). In some respects this is reminiscent of the comparison between sea nettles of the Gulf coast and Chesapeake Bay discussed earlier.

Differences along morphometric parameters on an intergeneric basis between Nemopsis bachei and Bougainvillia carolinensis are striking. Regression curves for number of oral tentacle branches, number of tentacles per bulb, bell cavity height, and bell diameter

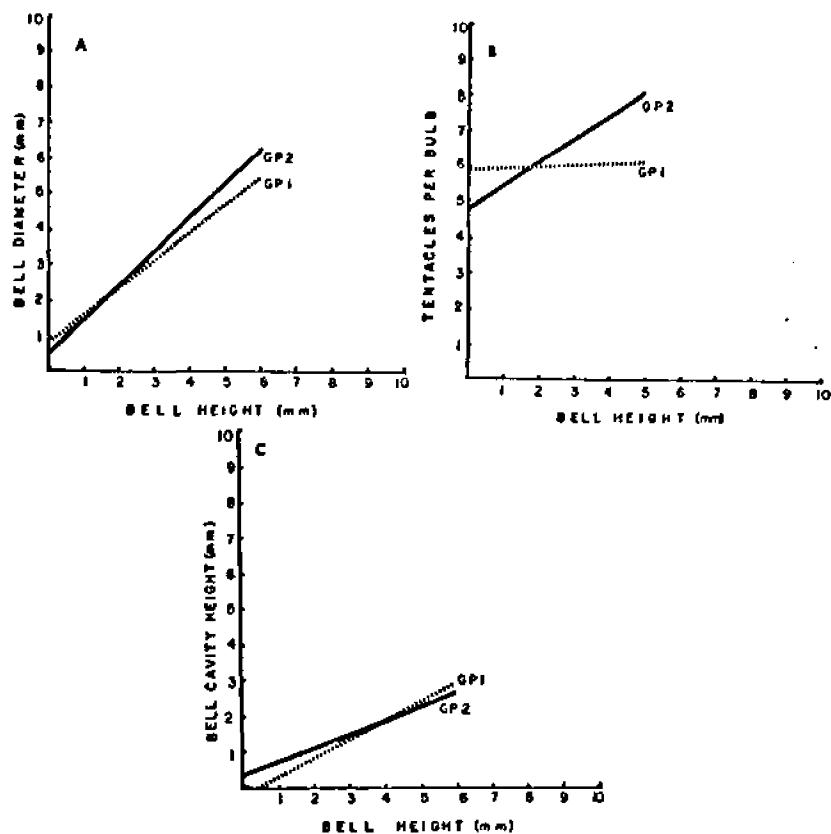


Figure 32. Regression curves for morphometric analysis of *Bougainvillia carolinensis*. GP 1 indicates Mississippi Sound population and GP 2 indicates merit population south of Mississippi Sound. Regression equations and correlation coefficients are given in Table 22.

versus bell height are shown in Figure 33. Correlation coefficients and other pertinent statistics for Nemopsis are given in Table 23.

From inspection of these results it is obvious that there is greater morphologic distance between the two genera than between the two populations of Bougainvillia carolinensis. The data with respect to hydrographic conditions and ecologic factors affecting medusa release are unknown in the northern Gulf for this medusa. The available collection data are inadequate for evaluation of ecologic relationships. In any event the morphological differences between the two populations of Bougainvillia carolinensis are very significant and indicate a certain degree of autonomy on a morphologic basis between the two populations. It is quite possible that the Mississippi Sound barrier islands constitute a significant geographic or ecological barrier allowing establishment of two differentiable populations of this medusa.

There are two possible explanations for the two subpopulations of B. carolinensis. It is possible that hydrographic factors affect stage at which the medusa is released from the hydroid and its resulting growth pattern. Secondly, the barrier islands may be envisioned as an isolating mechanism allowing subspeciation in the two areas. Elucidation of the correct explanation requires more intensive work with the hydroid stages of these medusae and laboratory study of medusa release and growth, as well as more field data related to occurrence of medusa swarms and comparison of individual swarms of medusae.

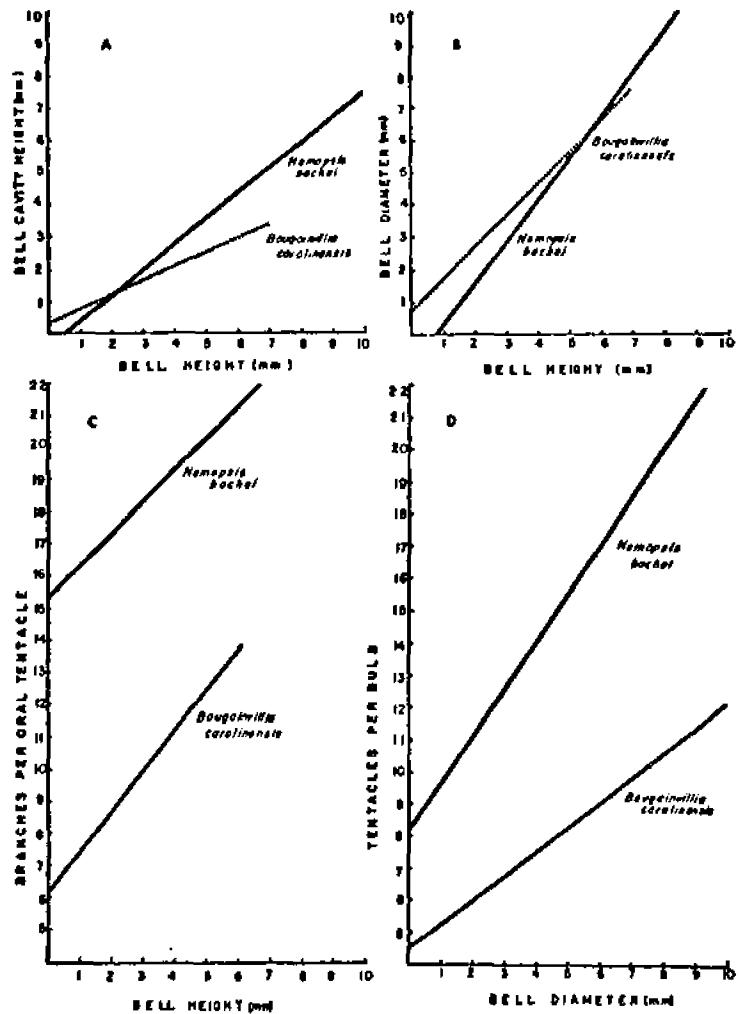


Figure 33. Regression curves for comparison of *Bougainvillia carolinensis* and *Nemopsis bachei*. Regression equations and correlation coefficients are given in Table 23.

### Siphonophora

#### General Account

Most species of siphonophores are cosmopolitan and only very few species are endemic in any one area. Forty-five species of siphonophores were encountered in the present study, this number being roughly one-third of the world number of valid species of siphonophorae. No new species were encountered, although eight species previously known only from the Indo-Pacific have been encountered in the Gulf. The siphonophores can, on a habitat basis, be divided into two groups. The first group discussed are those siphonophores taken in waters shallower than 60 fathoms; the second group is that taken in the oceanic habitat beyond the 100 fathom contour. Systematic species list and distribution, according to habitat, of the various siphonophores is given in Table 2 and 3. For the most part the neritic siphonophore assemblage consists of a depauperate oceanic fauna and those siphonophores in estuarine areas are accidental occurrences related to oceanic incursion and estuarine-neritic intermixing. Without exception Gulf of Mexico siphonophores are tropical-equatorial forms.

Of the 45 species of siphonophores encountered, 36 were taken by either meter nets or mid-water trawls by the R/V ALAMINOS, and 24 species were taken in neritic waters. Collection source for the various species is given in Table 3.

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#### Siphonophores in Mississippi Sound

Only two species of siphonophores are found with any regularity in the estuary. These are the Portuguese Man O' War, Physalia physalis, which may at times be blown into the sound in tremendous numbers, and the small, neritic calycocephoran Muggiaea kochi which, during summer months, may be found in Mississippi Sound proper along the north shores of the barrier islands. The occurrence of Muggiaea in the sound is obviously the result of an influx of neritic water from south of the barrier islands. It should be pointed out that although Physalia normally occurs in the Sound, the shallow conditions (average depth of Mississippi Sound being ten feet) cause its tentacles to drag and tear hastening the death of the organism. Muggiaea kochi is characteristically a neritic siphonophore and its occurrence in Mississippi Sound in a non-moribund stage is not surprising. Some areas of Mississippi Sound, i.e., those in the vicinity of the barrier island passes, at times have salinity and temperature regimes approaching those of offshore neritic waters. This allows for the occasional incursion of typically oceanic forms which include nectophores of Nanomia bijuga, Agalma okeni as well as polygastric and eudoxid stages of Diphyes dispar and Bassia bassensis. Specimens of these four species, when taken in the estuary, are typically moribund. The occurrence of these forms as accidental inhabitants of Mississippi Sound has been noted in an earlier paper (Phillips and Burke 1970).

Physalia physalis in the Northern Gulf

During April and May 1968, Portuguese Men O'War (Physalia physalis) were extremely abundant in Mississippi Sound. A similar infestation occurred during January and February 1969. These extremely noxious animals can be found in northern Gulf inshore waters whenever there are strong south winds and high salinities (25 o/oo or greater). Viable specimens have been taken at times in the upper reaches of coastal bayous. During April and May 1968 there was a considerable amount of local concern in the Mississippi Gulf Coast area with respect to several apparent cases of Physalia stings.

In May I was interviewed on the local television station in Biloxi with regard to the public health hazard posed by the Physalia influx. Following this television appearance numerous cases of Physalia attacks were reported to the Gulf Coast Research Laboratory. Only four of these supposed attacks could be authenticated by the concomitant capture of the Physalia or its tentacles. During the spring 1968 infestation, local interest reached such a fervor that daily calls from the Biloxi and Ocean Springs police and fire departments to the Gulf Coast Research Laboratory inquiring about the advisability of closing the local beaches were not at all unusual. It is somewhat ironic that the heavier 1969 infestation went relatively unnoticed by the local populace. This may have been due to the smaller amount of publicity given to it.

In both infestations literally thousands of specimens were washed up on Mississippi coastal and barrier island beaches. The occurrence

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of occasional swarms of Physalia does constitute a potential and very real hazard to the unwary bather, fisherman or naturalist.

Physalia of all size ranges were collected. In November and December 1968 early postlarval stages of Physalia were taken in offshore neritic waters. During January only adults were taken and of these 85 percent were left handed (*sensu* Totton 1960). Collection data, including float orientation, are given in Table 24. Additionally, long windrows of Physalia up to a mile in length were observed in Dog Keys Pass during the spring 1968 influx.

Physalia can exist as adults in one of two orientations, either sinistral or dextral (Figure 34). This handedness is readily apparent when float length reaches 10 mm. The predominant form taken in a given region is thought to be a function of wind conditions when the postlarval stage is reached (Woodcock 1956), the exact mechanism being very unclear. Totton (1960) and Mackie (1960) give excellent accounts of the natural history, morphology and histology of the Portuguese Man O'War. Although the great majority of the specimens taken in the present study are left handed (Table 24), the significance is unclear. It can be seen from Table 24 that there are no significant differences with respect to float dimorphism during either infestation. I am of the opinion that the dimorphism may have a genetic basis and that different swarms of Physalia in different water masses may have different frequencies of dextral and sinistral individuals as a result of particular selection factors in different breeding areas. Although there is obviously at least one breeding

TABLE 24  
 COLLECTION DATA FOR *Physalia physalis* IN THE NORTHERN GULF OF MEXICO  
 (Collecting sites correspond to stations shown in Figures 1 and 2.)\*

Date	Collecting Site	No. Specimens Measured	Measurements		Orientation	
			Size Limits (mm)	Mean Float Length (mm)	Lefthanded (%)	Righthanded (%)
4-4-68	St. 4 Inshore	3	30.0-40.0	34.66	0	100
4-4-68	South beach on West end of Horn Island	2	90.0-95.0	92.50	0	100
4-10-68	St. 48 Inshore	60	35.0-215.0	122.69	94.91	5.08
4-10-68	South beach on West end of Horn Island	38	13.0-180.0	95.23	97.36	2.63
5-15-68	St. 1 Inshore	20	120.0-220.0	174.55	174.55	50
5-16-68	South beach on West end of Horn Island	74	70.0-205.0	133.25	47.29	45.94
5-17-68	St. 1 Inshore	5	80.0-150.0	101.00	60	-
11-14-68	St. 5 Offshore	1		2.0	-	-
11-21-68	St. 4 Offshore	1		4.0	-	-
12-10-68	St. 4 Offshore	9	4.0-8.0	6.11	-	-

TABLE 24 (Continued)  
 COLLECTION DATA FOR *Physalia physalis* IN THE NORTHERN GULF OF MEXICO  
 (Collecting sites correspond to stations shown in Figures 1 and 2.)\*

Date	Collecting Site	No. Specimens Measured	Measurements		Orientation	
			Size Limits (mm)	Mean Float Length (mm)	Lefthanded (%)	Righthanded (%)
12-10-68	St. 5 Offshore	12	3.0-7.0	5.7	-	-
12-10-68	St. 5 Offshore	1		6.0	-	-
12-10-68	St. 6 Offshore	4	4.0-8.0	6.00	-	-
1-14-69	St. 4 Offshore	2	60.0-60.0	60.0	100	0
1-23-69	St. 4 Offshore	5	70.0-110.0	84.0	100	0
1-23-69	St. 6 Offshore	4	55.0-150.0	106.6	100	0
1-31-69	St. 48 Inshore	6	70.0-170.0	115.83	100	0
1-31-69	South beach on West end of Horn Island	156	20.0-180.0	105.03	100	0
2-4-69	St. 1 Inshore	8	50.0-170.0	114.37	62.50	37.50
2-4-69	St. 4 Inshore	14	65.0-160.0	110.35	100	0
2-5-69	St. 4 Inshore	13	30.0-170.0	111.53	100	0
2-5-69	South beach on Deer Island	6	105.0-195.0	160.83	100	0

TABLE 24 (Continued)  
 COLLECTION DATA FOR *Physalia physalis* IN THE NORTHERN GULF OF MEXICO  
 (Collecting sites correspond to stations shown in Figures 1 and 2.)\*

Date	Collecting Site	No. Specimens Measured	Measurements		Orientation	
			Size Limits (mm)	Mean Float Length (mm)	Lefthanded (%)	Righthanded (%)
2-6-69	St. II Inshore	28	20.0-150.0	95.35	85.71	14.28

\*Note: Dashes and residual percentages indicate those situations in which orientation could not be determined.

population of Physalia in the Gulf of Mexico, virtually nothing is known on the distribution of the various swarms, reproductive frequency, growth and population dynamics.

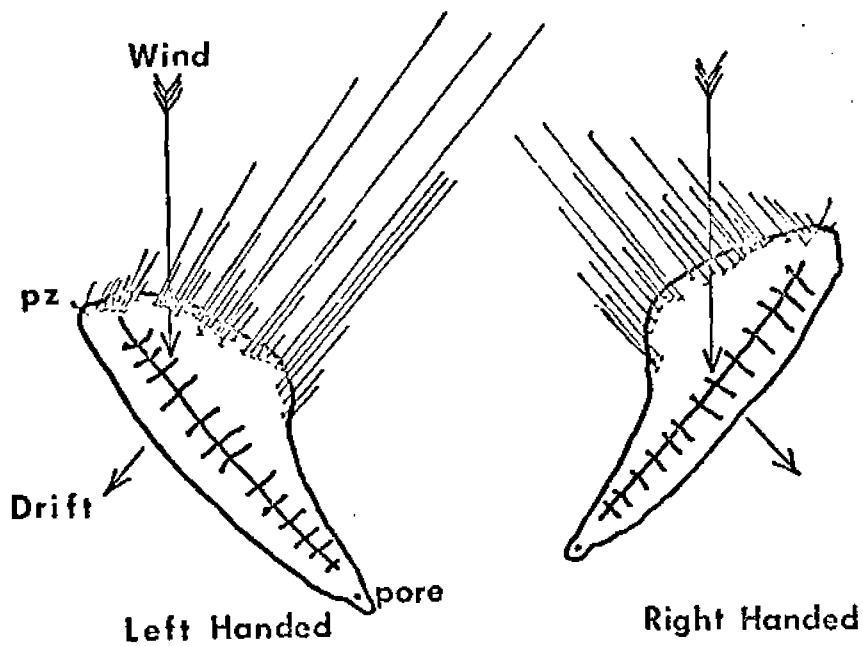


Figure 34. Float orientation in Physalia physalis. Drift in relation to wind direction is indicated. Asymmetry is a result of the basal bulge of the float whereon the cormidial groups are attached. PZ indicates primary zooid. (After Totton 1960).

#### Siphonophores in Water Shallower Than 60 Fathoms

The ecologic distribution of siphonophores in the Gulf of Mexico with respect to depth as well as neritic and oceanic habitat is given in Table 2. Table 25 shows the monthly occurrences of siphonophores at the 5, 10, 20, 30, 40 and 50 fathom curves off the Mississippi Coast (Figure 2), designated Stations 1 through 6 respectively. For calycocephoran siphonophores frequencies of eudoxid and polygastric stages are given in Table 26, along with the numerical abundance of each species in neritic waters. A total of 25 species was encountered in northern Gulf coastal waters.

As can be readily seen from the data in Table 25 there is a distinct paucity of siphonophores at the 5 fathom locality (Station 1) immediately south of Dog Keys Pass. This is obviously due to the estuarine conditions present at this station. The only form found here in any numbers is Muggiaea kochi which is the only truly neritic siphonophore found in the Gulf of Mexico. The other three species taken consisted of isolated moribund specimens. The siphonophore complement at this station is almost identical with that discussed for Mississippi Sound. As can be seen from Table 25, siphonophoran species diversity increases with increasing distance from the shoreline. Stations 1, 2 and 3 were sampled more often and with greater regularity than Stations 4, 5 and 6 thus accounting for the greater species diversity at Station 3 as compared with Station 4. Salinity and temperature distribution for each of the forms encountered in neritic waters is given in Tables 27 and 28.

TABLE 25

SEASONAL OCCURRENCE OF SIPHONOPHORES IN THE NORTHERN GULF OF MEXICO  
(X indicates polygastric generation; 0 indicates free eudoxid generation; P indicates presence of noncalycophoran siphonophores.)

Species	—1967—			—1968—			—1969—									
	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1
<u>Station 1</u>																
<u>Abylopsis tetragona</u>	X															
<u>Erenesconium hvalium</u>	0															
<u>Muggiaea kochii</u>																
<u>Diphyes dispar</u>								X	X	X	X	X	X			
								X0	X0	X0	X0					
<u>Station 2</u>																
<u>Abylopsis eschscholtzii</u>	X0	0	X0													
<u>Abylopsis tetragona</u>	X0	X0	X0	X0		X	X0	X0								X0
<u>Arsalma okenii</u>																P
<u>Bassia bassensis</u>	0	X0	X0	X0		X	X0	X0								X0
<u>Diphyes boianus</u>	X0	X0	X	X		X	X0	X0								X0
<u>Diphyes dispar</u>	X0	X0	X	X0		X0	X	0				X0	X0			
<u>Erenesconium hvalium</u>	0	0	X0	0		0										
<u>Muggiaea nitra</u>	0															
<u>Sudexoides spiralis</u>		X0	X0	X0		0						0	X			
<u>Muggiaea kochii</u>	X				X	X	X	X	X	X	X	X	X			X
<u>Nanomia bilineata</u>					X											
<u>Station 3</u>																
<u>Abylopsis eschscholtzii</u>	X0	X0		X	0							0		X	0	
<u>Abylopsis tetragona</u>	X0	X0		X0	X							0		0		I

TABLE 25 (Continued)  
SEASONAL OCCURRENCE OF SIPHONOPHORES IN THE NORTHERN GULF OF MEXICO  
(X indicates polygastric generation; O indicates free eudoxid generation; P indicates presence of nonalcydian siphonophores.)

TABLE 25 (Continued)  
 SEASONAL OCCURRENCE OF SIPHONOPHORES IN THE NORTHERN GULF OF MEXICO  
 (X indicates polygastric generation; O indicates free eudoxid generation; P indicates presence of noncalycophoran siphonophores.)

Species	—1967—			1968			—1969—									
	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1
<u>Station 4 (Continued)</u>																
<u>Aralma okeni</u>												X				
<u>Bassia bassensis</u>	XO				XO			XO	XO	XO	XO	XO				
<u>Chelochves appendiculata</u>	X							XO			X	X				
<u>Diphyes bojani</u>	XO				XO			O	O			XO				
<u>Diphyes dispar</u>	XO				O			XO	XO	XO	XO	XO				
<u>Fimbragonium hyalium</u>	O							O								
<u>Lamia spp.</u>																
<u>Lewisia campanella</u>												X				
<u>Muricea kochi</u>	X							X	X	X	X	X				
<u>Sulceolaria spp.</u>											X	X				
<u>Station 5</u>																
<u>Abulopsis eschscholtzii</u>	XO							O	O		O	O				
<u>Abulopsis tetracona</u>	XO							XO	XO							
<u>Aralma okeni</u>										P	P					
<u>Archicaryon aculea</u>	X															
<u>Bassia bassensis</u>	XO				XO			O	X	XO	XO	XO				
<u>Chelochves appendiculata</u>	X				X			X	XO	X	X					
<u>Dipalma cordiformis</u>									P							
<u>Diphyes bojani</u>	XO				O			O	XO	XO	XO	XO				
<u>Diphyes dispar</u>	XO				XO			XO	XO	XO	XO	XO	XO			
<u>Fimbragonium hyalium</u>	O								XO		O					

TABLE 25 (Continued)

## SEASONAL OCCURRENCE OF SIPHONOPHORES IN THE NORTHERN GULF OF MEXICO

(X indicates polygastric generation; 0 indicates free eudoxid generation; P indicates presence of noncalycophoran siphonophores.)

Species	—1967—				—1968—				—1969—							
	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1
<u>Station 5 (Continued)</u>																
<u>Eudoxoides mitra</u>					0		0			X	0	X	X	X		
<u>Eudoxoides spiralis</u>					X0					X0	X0	X0	X0			
<u>Hippocodius hippocampus</u>					X											
<u>Lensia</u> spp.								X								
<u>Lensia campanella</u>										X				X		
<u>Lensia challengerii</u>						X										
<u>Murcielaca</u> kochii								X		X		X				
<u>Nanomia</u> bijunga						X										
<u>Sulculeolaria</u> spp.					P							P		P		
<u>Sulculeolaria</u> chuni					X						X	X				
<u>Sulculeolaria quadrivalvis</u>							X					X				
<u>Station 6</u>																
<u>Abulopsis eschscholtzii</u>	X0				X0		X0			0	X0	0	0			
<u>Abulopsis tetragona</u>	X0				X0		X			0	X	0		X0		
<u>Apolma okeni</u>						P	P						P			
<u>Amphicarpon ernestii</u>												X				
<u>Amphicarpon peltifera</u>						X										
<u>Bassia bassensis</u>	X0				X0		X	X0		X0	X0	X0	X0			
<u>Chelopsis appendiculata</u>	X				X0		X			X	X0	X0	X			
<u>Ceratocydya luecarti</u>														X		
<u>Cerianatulma cordiformis</u>												P				

TABLE 25 (Continued)

## SEASONAL OCCURRENCE OF SIPHONOPHORES IN THE NORTHERN GULF OF MEXICO

(X indicates polygastric generation; 0 indicates free eudoxid generation; P indicates presence of noncalycocephoran siphonophores.)

Species	—1967—			1968			—1969—									
	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1
<u>Station 6 (Continued)</u>																
<u>Diphyes bojani</u>	XO			XO		0	0	0	0	0	XO		XO			
<u>Diphyes dispar</u>	XO			XO		0		XO	XO	XO	XO		XO			
<u>Phaezonium hvalium</u>	XO			0		XO		0		0		0				
<u>Eudoxoides mitra</u>				XO				0		XO			X			
<u>Eudoxoides spiralis</u>	X			XO		X	XO		XO	XO	X		XO			
<u>Lensia spp.</u>							X					X		X		
<u>Lensia carmenella</u>						X						X		X		
<u>Lensia subtilis</u>							X									
<u>Muricea Kochi</u>	X			X						X	X					
<u>Rhizopysa filiformus</u>				P												
<u>Sulculesilaria sp.</u>	X			X			X			X	X	X				
<u>Sulculesilaria chuni</u>				XO												
<u>Sulculesilaria quadrivalvis</u>	X			X	X			X	X							
<u>Stations 1-6 pooled</u>																
<u>Abylopsis eschscholtzi</u>	XO	XO	XO		XO	0	XO	0	0	0	XO	0	0	XO	0	0
<u>Abylopsis tetragona</u>	XO	XO	XO	XO	X	XO	XO	X	X	0	X	0	XO	XO	XO	XO
<u>Acalma ekoni</u>				P		P	P	P				P	P	P	P	P
<u>Aphicarpon ernestii</u>	X			X	X						X	X	X	X	X	X
<u>Aphicarpon acaule</u>						X							X			
<u>Cyanea bassensis</u>	XO	XO	XO	XO		XO	XO	XO	XO	XO	XO	XO	XO	XO	XO	XO
<u>Diphyes appendiculata</u>	X	X	X	X		XO	X	X	XO	X	XO	XO	X			

TABLE 25 (Continued)  
 SEASONAL OCCURRENCE OF SIPHONOPHORES IN THE NORTHERN GULF OF MEXICO  
 (X indicates polygastric generation; O indicates free eudoxid generation; P indicates presence of noncalycothorac siphonophores.)

Species	1967				1968				1969							
	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1
<u>Stations 1-6 pooled (Continued)</u>																
<u>Ceratocymba lucarti</u>																X
<u>Corydalis cordiformis</u>															P	P
<u>Diphyes bojani</u>	XO	XO	X	XO		XO	XO	XO	O	O	O	O	XO	XO	XO	XO
<u>Diphyes dispar</u>	XO	XO	X	XO		XO	XO	XO	XO	XO	XO	XO	XO	XO	XO	XO
<u>Fornicinum bivalium</u>	XO	XO	XO	O	O	O	XO		O	O		XO	O	O	XO	
<u>Eudoxoides nitra</u>	O	O		XO		XO			O	O	XO	XO	X	XO		
<u>Eudoxoides spiralis</u>	XO	XO	XO	XO	XO			XO	XO		XO	XO	XO	XO	X	
<u>Hippocampus hippocampus</u>					X	X										
<u>Lensia spp.</u>	X								X		X	X	X			
<u>Lensia campanella</u>	X					X					X	X			X	
<u>Lensia challengeri</u>									X							
<u>Lensia subtilis</u>						X										
<u>Mesainaea kochii</u>	X	X		X		X	X	X	X	X	X	X		X	X	X
<u>Nemoria bijuga</u>					P		P									
<u>Rhynchocoelus filiformis</u>						P										
<u>Sclerularia sp.</u>	X		X	X	X	X		X			X	X	X	X		
<u>Sclerularia chuni</u>					XO						X	X				
<u>Sulculesolaria quadrivalvis</u>					X	X	X				X	X		X		

TABLE 26  
FREQUENCY OCCURRENCE OF IDENTIFIED CALYCOPHORAN SIPHONOPHORES IN MISSISSIPPI COASTAL WATERS

Species	Polygastric		Free Eudoxid		Total Percentage
	Number	Percentage	Number	Percentage	
<i>Diphyes dispar</i>	3764	59	2636	41	22
<i>Diphyes bojani</i>	2720	52	2484	48	18
<i>Muricea kochi</i>	5022	100	0	0	17
<i>Chelophyes appendiculata</i>	4731	98	100	2	16
<i>Bassia bassensis</i>	1657	46	1881	54	12
<i>Abylopsis eschscholtzii</i>	92	9	885	91	4
<i>Eudoxoides spiralis</i>	775	70	310	30	4
<i>Entacmaea hyalinum</i>	165	24	518	76	2
<i>Abylopsis tetragona</i>	343	68	163	32	2
<i>Saliculeolaria quadrivalvis</i>	224		fragments	224+	< 1
<i>Saliculeolaria</i> sp.	200		fragments	200+	< 1
<i>Amphicarpon ernestii</i>	14	100	0	0	14
<i>Ceratocymbe leuckartii</i>	1	25	3	75	4
<i>Saliculeolaria chuni</i>	3		fragments	3	< 1
<i>Amphicarpon peltifera</i>	2	100	0	0	2
<i>Hippopodius hippocampus</i>		fragments			

Total number of calycophoran siphonophores = 29,045

**TABLE 27**  
 TEMPERATURE AND SALINITY RANGES FOR SIPHONOPHORES IN  
 MISSISSIPPI COASTAL WATERS

<u>Species</u>	<u>Salinity (o/o)</u>		<u>Temperature (C)</u>	
	Minimum	Maximum	Minimum	Maximum
<u>Abylopsis eschscholtzi</u>	28.9	36.5	15.3	29.3
<u>A. tetragona</u>	23.6	36.5	15.1	29.8
<u>Bassia bassensis</u>	23.3	38.8	15.2	29.2
<u>Chelophyes appendiculata</u>	31.5	36.5	15.1	29.3
<u>Diphyes bojanii</u>	28.2	36.5	15.1	29.3
<u>D. dispar</u>	23.3	36.7	13.3	29.2
<u>Enneagonium hyalinum</u>	24.4	36.8	13.3	29.2
<u>Eudoxoides mitra</u>	31.5	36.5	19.9	24.1
<u>E. spiralis</u>	31.5	36.4	13.3	29.2
<u>Lensia campanella</u>	25.9	36.4	21.3	27.5
<u>Muggiaeae kochii</u>	23.6	36.4	15.2	31.0
<u>Sulculeolaria chuni</u>	28.2	34.0	25.0	26.2
<u>Sulculeolaria quadrivalvis</u>	21.6	35.7	16.8	28.5
<u>Amphicaryon peltifera</u>	23.2	34.9	15.4	16.8
<u>Amphicaryon ernestii</u>	27.0	38.2	15.1	26.0

TABLE 28  
TEMPERATURE DISTRIBUTION OF SIPHONOPHORES IN THE NORTHERN GULF OF MEXICO

(The number without brackets indicates polygynous anterior ectophores; the number in brackets designates eudoxid bracts.)

Species	Temperature (°C)																	
	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<u>Diphyes dispar</u>	9 (7)	58 (120)		170 (1020)(103)	91 (385)		160 (46)	62 (93)	167 (240)	144 (239)		150 (84)	56 (306)	416 (269)		1309 (109)		
<u>Diphyes botani</u>	9 (24)		35 (10)	16 (40)		26 (111)	20 (60)	128 (129)	192 (208)			10 (20)	20 (98)	2275 (1511)				
<u>Mosima kochi</u>	38		1	30	10		2	59	3355 (3355)	773 (773)		306 (306)	30 (30)	108 (108)		270 (270)		
<u>Chelophores appendiculata</u>							14	5	120 (110)	144 (16)		12	96 (74)	30 (14)	4255 (53)			
<u>Rissoa hassensis</u>	3 (6)	58 (80)	524 (512)		10 (30)	154 (227)	7 (34)	61 (34)	72 (36)	40 (35)	164 (35)	64 (74)	12 (14)	40 (53)	170 (233)			
<u>Abuloxia escharinolexi</u>					5 (24)		8 (5)	1	48 (96)		48 (45)		10 (76)	30 (69)	120 (120)		30 (35)	
<u>Abuloxia tetragona</u>	5 (1)	6 (2)		1	15 (25)	16 (3)		38 (10)	130 (22)	61 (45)	48 (48)		1		70 (2)			
<u>Fidicinaea strobilina</u>	2 (10)	45 (15)	96 (97)		45 (10)	16 (8)		40 (16)	88 (62)	140 (45)	48 (34)				235 (10)			
<u>Tubularia nitra</u>								16 (2)	12 (5)	11 (20)	48 (11)				14 (48)			
<u>Enneanema hispidum</u>	0 (0)	12		120 (45)		3 (96)		3 (9)	81 (81)	1	16 (16)		5		30 (99)		11 (11)	
<u>Sulcocalularia quadrivalvis</u>					1					1	4	1	2	24	200			
<u>Sulcocalularia chani</u>											2	1						
<u>Lentia campanella</u>								8		5	1		13					

As opposed to coastal leptolinid medusae, siphonophores have rather narrow salinity tolerances, preferring rather high salinity waters. Temperature and salinity interaction as related to siphonophore distribution in northern Gulf coastal areas is unclear from the present data; however, it is fairly obvious that greater abundance is related to higher salinities and to temperatures higher than 20 C. These conditions can possibly be correlated with the incursion of tropical oceanic surface waters. Temperature distribution frequencies obtained for northern Gulf coastal siphonophores (Table 28) are comparable with those reported by Bigelow and Sears (1937) for Mediterranean and Western Atlantic populations.

Moore (1953) attempted to define water mass type, especially Florida Current water, on the basis of siphonophore complement. Since Moore gives no account of the method used to quantitate polygastric and eudoxid stages his data are questionable. Moore (1953) claims to have worked out reproductive cycles and to have demonstrated differences in eudoxid and polygastric stages of particular species in different water masses. His data on these points, since no method for quantification is given, are muddled at best. No size ranges or other pertinent data with respect to sex ratios or reproductive stages are given. Although quantitative records were kept for all stages of each species in the present study, the data are insufficient for determining reproductive cycles in northern Gulf waters. With respect to using siphonophores as indicator organisms in coastal waters the only valid account in the

literature is that by Russell (1934) wherein accounts of Muggiae atlantica and M. kochi in the English Channel are given.

With respect to northern Gulf coastal waters Muggiae kochi was one of the five most abundant forms (Table 26) accounting for 17 percent of the total siphonophore population. Oddly enough Moore (1953) did not report M. kochi from Floridian coastal waters. Muggiae is an excellent indicator of neritic water in the Gulf as well as other areas. It is easily quantitated and can be used as a quantitative index of estuarine flushing or incursion of neritic water into the oceanic epipelagic zone. No Muggiae were taken beyond continental shelf areas in the present study. Although Abylopsis tetragona was taken with much greater frequency than its sibling species A. eschscholtzi in the oceanic environment (Issacs-Kidd midwater trawl samples and meter net samples), A. eschscholtzi was six times as abundant as A. tetragona in northern Gulf coastal waters, accounting for 12 percent of the total calycoptile population in this subregion. Evidently A. eschscholtzi is typically more neritic than A. tetragona and relative frequencies of the two species should be an excellent quantitative indicator of coastal conditions. Lensia challengerii and L. subtilis at least in the present study are restricted to continental shelf areas.

Other features peculiar to coastal siphonophores are the generally smaller size of some forms in comparison with their oceanic counterparts. Abylopsis tetragona in coastal waters varies from 4 to 12 mm in polygastric length (anterior plus posterior nectophore)

whereas in open Gulf waters specimens 15 to 20 mm in length are common. This is particularly true with respect to Sulcogelaria quadrivalvis. Anterior and posterior nectophores of this species from coastal areas are seldom larger than 12 to 15 mm respectively, whereas those taken in Isaacs-Kidd midwater trawls or meter nets usually exceeded 20 and 22 mm respectively, nectophores of both types in excess of 24 mm being quite common.

Other features of unusual interest with regard to coastal siphonophores include the occurrence of Amphicaryon peltifera. Collection data for Amphicaryon peltifera and Amphicaryon ernesti in northern Gulf coastal waters are given in Table 29. Although Amphicaryon acaule is common in the open Gulf none were taken in coastal areas. More work regarding the distribution of this genus in the Gulf is needed before any conclusive statements can be made on its ecology. It should also be noted that relatively few agalmids were taken in coastal areas and those that were taken consisted mainly of isolated nectophores and early postlarval stages. The only cystonects other than Physalia encountered in this study were adult specimens of Rhizophysa filiformis found only occasionally in the neritic samples and encountered only once in the oceanic collections.

In essence the neritic or coastal siphonophores of the northern Gulf of Mexico constitute a somewhat depauperate oceanic fauna having at least one indigenous element (Muggiae kochi) and characterized by a greater abundance of certain forms (Abylopsis eschscholtzii and two species of Lensia). In my opinion analysis of the siphonophore

population structure of coastal areas can be related to rates of estuarine or river discharge, and estuarine outflow or flushing can be quantitated on the basis of the siphonophore and medusa community structure. Alvarino (1968) demonstrated that the distribution patterns of the various species of chaetognaths, siphonophores and hydromedusae could be directly related to Amazon outflow, the Atlantic tropico-equatorial species appearing in highest density when the Amazon River outflow was at a minimum. Siphonophores and medusae have been virtually unused tools to measure movement of coastal water in the Gulf of Mexico.

TABLE 76  
COLLECTION DATA FOR ASSOCIATED MEDUSAE AND A. ZEGLERII IN WATERS ADJACENT TO MISSISSIPPI RIVER

Date	Station	Sample No.	No. Spec.	Type	Salinity		Temperature	
					Surface	Bottom	Surface	Bottom
<b>A- medusae</b>								
3-27-66	6	13	1	polycysteic	23.4	23.2	17.4	15.4
12-10-66	3	33	1	polycysteic	23.1	24.9	16.5	14.8
<b>A- medusae</b>								
10-27-67	1	16	1	polycysteic with developing oocytes	34.5	36.7	24.1	22.3
1-12-68	2	19	1	polycysteic	20.1	19.3	13.7	13.1
3-2-68	4	15	1	polycysteic	23.6	21.0	13.6	12.8
3-12-68	4	20	1	vertical levelling oocysts	33.7	35.7	21.6	20.0
10-9-68	3	10	1	vertical	25.7	28.7	23.6	21.6
10-9-68	6	29	1	polycysteic	27.3	30.2	27.6	25.2
10-12-68	3	15	2	polycysteic	34.9	36.3	20.1	19.3
11-1-68	2	29	1	polycysteic	33.3	35.7	20.4	20.7
11-10-68	3	26	1	vertical medusae with gonophore	37.4	36.9	21.8	21.8
<b>B-22-69</b>								
	6	36	2	polycysteic	35.2	34.5	17.3	15.0

### The Siphonophores of the Oceanic Environment

The eight species of siphonophores reported from the Atlantic for the first time with the exception of Aphicaryon ernesti and A. peltifera were found only in Isaacs-Kidd midwater trawl samples taken by the R/V ALAMINOS. Five of the remaining six species (Maresearia praecincta, Nectopyramis diomedae and Nectopyramis natans, Prava dubia and Clausophyes ovata) are calycocephorans. The remaining species, Marrus orthocannoides, is known in the Gulf from four nectophores.

With respect to bathymetric distribution little can be said because very few at depth midwater trawl samples were taken. It appears that Physophora hydrostatica, Halistemma rubrum, Nectopyramis diomedae, Nectopyramis natans, Clausophyes ovata, Chuniphyes dentata, Frenna richardi, Marrus orthocannoides and Bargmania elongata are encountered primarily in deeper water layers (below 1000 m). Although Bargmania elongata was taken in epipelagic samples taken by NMFS (cf. Tables 2 and 3) the largest nectophores were encountered in midwater trawl samples which had fished in the bathypelagic zone. Conversely this difference in size range (8 mm) may be related to size of the sampling device, particularly mouth opening.

Siphonophores in the oceanic zone are typically larger than specimens of the same species taken in neritic waters.

**Individual Accounts**

Rhizopysa filiformis  
Figures 35 and 36

Material. One specimen taken at  $28^{\circ}03'N$ ,  $94^{\circ}43'W$ , 27 August 1966  
by the R/V ALAMINOS at the surface

Remarks. Numerous specimens of Rhizopysa filiformis were taken in Mississippi coastal waters. Only one specimen, however, was taken anywhere else in the Gulf by the R/V ALAMINOS. Although specimens of up to three feet in length are known (Totton 1965) none of the present specimens exceeded 4 cm. Float dimensions varied from 2 to 5 mm in length. The apical pore and the hypocystic villi (Figure 35) are very prominent. The arrangement of the gastrozooids, tentacles and gonodendra are as described by Totton (1965). A cluster of gonophores about a nectophore is shown in Figure 36.

Bargmania elongata Totton 1954

Material. R/V ALAMINOS: Collection 12, 12 nectophores.

Remarks. The examined material is excellently preserved and there is no doubt about the identification of the isolated nectophores. Additional nectonhores have been encountered in other plankton samples taken in the Gulf. Pertinent morphometrics of the examined specimens are given in Table 39. Length ranged from 6 to 15 mm and breadth ranged from 2 to 6 mm.

These nectophores are easily recognized in the plankton by their lateral compression, especially of the nectosac (Totton 1965). The unlooped radial canals are diagnostic of this genus. Morpho-



Figure 35. Rhizophysa filiformis: Float (4 mm length). Note highly pigmented epidermal cells near apex and hypocystic villi below.



Figure 36. Rhizophysa filiformis: Cluster of gonophores about a nectophore and an isolated gonophore. The gonophore is 2 mm in length.

logically the present specimens are almost identical with those discussed by Totten (1954) from the "Discovery" collections. Although nectophores of this species are common in the Gulf I have not as yet encountered any complete specimens or siphosomal fragments.

TABLE 30  
MEASUREMENTS OF *Rargmania elongata* NECTOPHORES  
FROM THE GULF OF MEXICO

Length	Breadth
12.0	6.0
6.0	2.0
10.0	4.5
14.0	6.0
13.0	6.0
11.0	5.0
10.0	4.0
8.0	3.0
12.0	6.0
Mean =	11.7

Frenna richardi Redot 1904

Material. R/V ALAMINOS: Collection 5, 1 nectophore and 1 gastrozooid. Collection 7, in excess of 100 nectophores and 30 gastrozooids

Remarks. I am very much indebted to Dr. A. Alvarino for identification of these nectophores. Although the present specimens are much distorted by shrinkage and twisting, the presence of the typical black pigmented canals distinguish the identity of the nectophores. According to Alvarino (personal communication),

species is cosmopolitan, being found mainly at meso- and bathypelagic levels. Dr. Alvarino records finding this form in the upper 200 m in a region of strong upwelling in the Sea of Cortes and has taken a complete colony off Baja California. Alvarino (1964) has observed it in the western part of the Indian Ocean, the Philippine region and Indonesian Seas. Other areas from which this agalmid has been taken include the Azores, Bay of Biscay, Canary Islands, off Cabo Finisterre (Spain), S. of the Galapagos Islands, S. E. of Hawaii and in the Antarctic region.

The present nectophores range up to 18 mm in breadth. The mesogloea has a distinct pinkish tint. The gastrozoids are large (up to 25 mm in length); they have a distinct black pigmentation in the endoderm with a pinkish coloration in the remaining tissues. Morphologically they closely resemble the description given by Totton (1965).

Marrus orthocannoids Totton 1954  
Figure 37

Material. R/V ALAMINOS: Collection 10, 4 nectophores

Remarks. The present nectophores, up to 8 mm high, although somewhat twisted are clearly recognizable by the straight lateral radial canals which do not form sigmoid loops (Figure 37). Other than the nectophores no fragments of this species were taken in the present collection. This is the first record of this form in the western Atlantic. Additionally, this agalmid has been reported from the Indian Ocean (Alvarino 1964) and from south and east

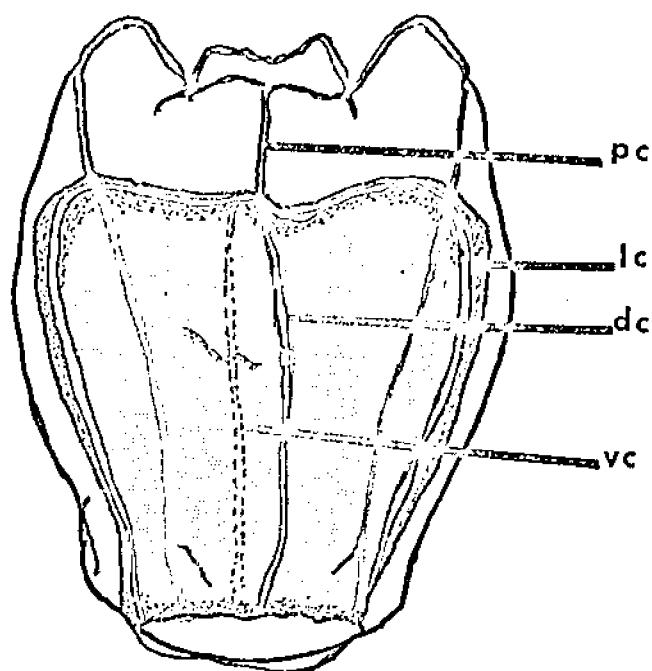


Figure 37. *Marrus orthocannoides*: Dorsal view of nectophore (6 mm high). p.c. indicates pedicular canal; l.c. indicates lateral radial canal; d.c. indicates dorsal radial canal; v.c. indicates ventral radial canal. Stippling designates muscular lamellae of nektosac.

African waters (Totton 1954). This form appears to be cosmopolitan in the deeper water masses.

Physophora hydrostatica Forskal 1775  
Figure 38

Material. R/V ALAMINOS: Collection 14, 1 complete specimen

Remarks. This is an extremely distinctive short-stemmed physonect that can be immediately identified by its characteristic pneumatophore with hypertrophied, sac-like siphosome (Figure 38). The float is elongate with a basal pore.

The present specimen has a total length of 26 mm with a float length of 11 mm. Height and breadth of the 6 nectophores are as follows:

Height	Breadth
13.5	16.0
16.0	15.5
14.0	14.0
13.0	10.0
14.0	14.0
13.0	13.0

The nectosome is only 5 mm in length. The siphosomal budding zone is in the form of a sac 16 mm in maximum dimension. The palpons are not evenly disposed in a clockwise spiral as described by Ruxley (1859), although a clockwise origin is indicated by the disposition of the smaller palpons. The smallest palpon (on the upper surface of the siphosome near its origin in Figure 38) and several of the other small palpons which form a clockwise spiral are interspersed by several larger, older palpons. This indicates



Figure 38. *Physophera hydrostatica*. Float length is 11 mm. b.p. indicates basal pore of float; b.r. indicates bract; g.d. indicates gonodendra; g.z. indicates gastrozooid; nect. indicates nectosome; p. indicates pneumatophore (float); pl. indicates palpon; slph. indicates siphon.

that the budding of the siphosome in the present specimen is uneven and somewhat anomalous when compared to that illustrated by Haeckel (1888), and by Bigelow and Sears (1935) and discussed by Totton (1954 and 1965). The arrangement of the gastrozooids is distinctly clockwise in ascending magnitude.

According to Totton (1965) this species is cosmopolitan and has a known temperature range of 3 to 21.1 C. No data are available regarding its temperature range and bathymetric distribution in the Gulf of Mexico.

Maresearsia praeclarus Totton 1954  
Figures 39-41

Material. R/V ALAMINOS: Collection 7, one complete specimen

Remarks. This is the first report of this species which previously has been reported from the Indian Ocean, possibly indicating this may be a cosmopolitan form.

The dimensions of the present specimen are given below.

Definitive Nectophore (Figures 39 and 40)

distance from ostium of nectosac to	
opening of hydroecium:	14 mm
diameter	19 mm
length of somatocyst	5 mm

Vestigial Nectophore (Figure 41A)

distance from ostium of nectosac to	
siphosome:	6 mm
diameter	10 mm

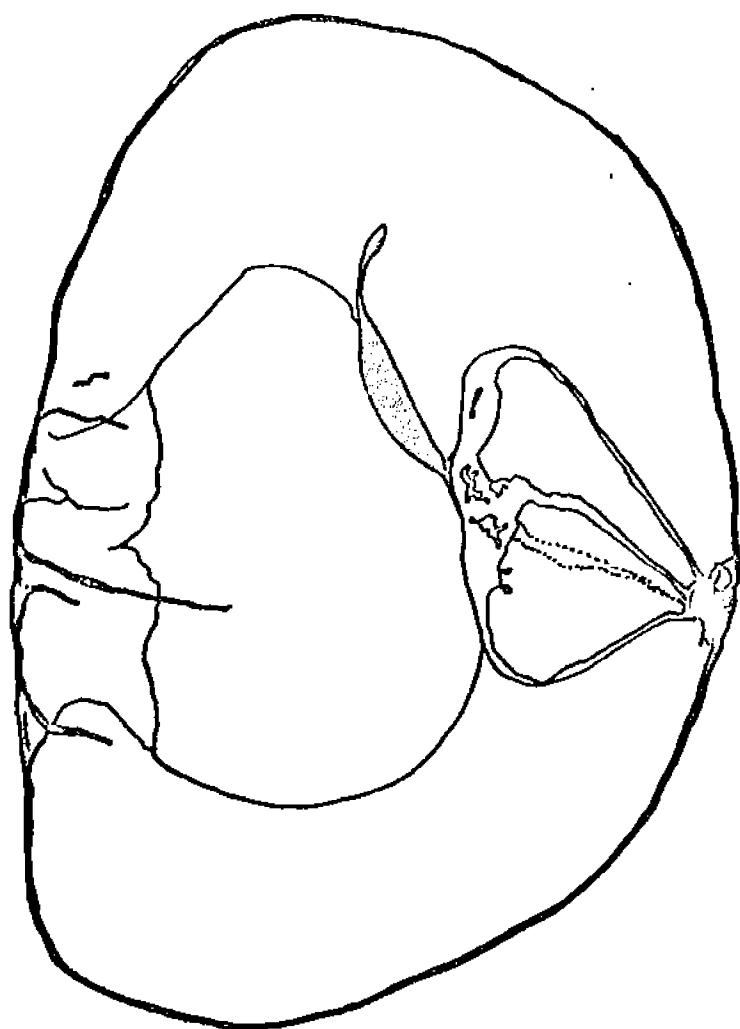


Figure 39. *Marsecarsia praeclarat*. Definitive nectophore (lateral view). Maximum diameter is 19 mm.

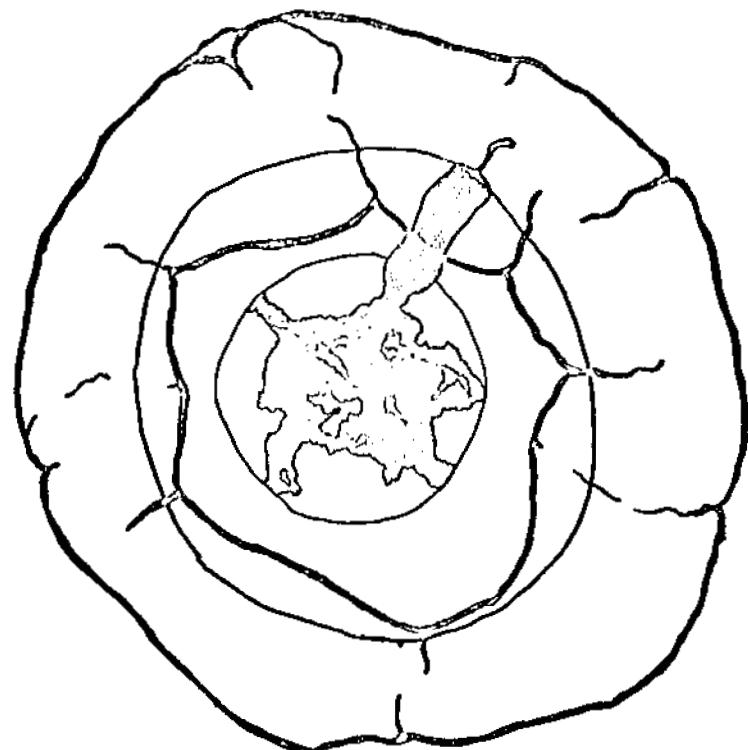


Figure 40. *Marescursia praeclara*: Definitive nectophore  
(aboral view). Maximum diameter is 19 mm.

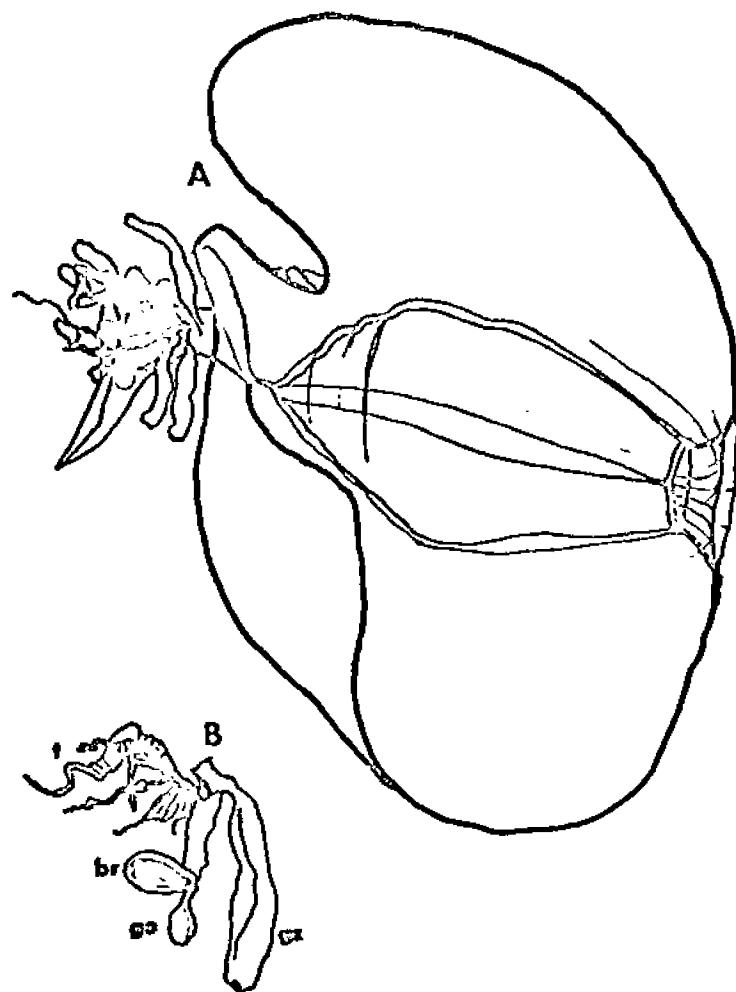


Figure 41. *Marecaaria praeclarra*: Interior nectophore and eudoxoids.  
A is an inferior nectophore (10 mm maximum diameter);  
B is an individual endoxoid showing tentacle (t) with attached tentillae; bract (br) with attached gonophore (go) and the gastrozooid (gz).

This genus is easily distinguished from Amphigaryon by the presence of a well developed nectosac in both nectophores. The canal network of the definitive, larger nectophore is characterized by an irregular anastomosis at the apex of the nectosac (Figure 61).

The eudoxoid, which I have not encountered free in the plankton, has a characteristic bracteal canal system consisting of three horn-like branches (Figure 41B).

Nectopyramis diomedae  
Figure 42

Material. R/V ALAMINOS: Collection 7, 1 bract 20 mm high  
Collection 18, 1 bract (30 mm high, 22 mm wide) taken with a closing device at a depth of 2475 m

Remarks. This species is easily distinguished from all other members of this genus by the characteristic branching of the canal system (Figure 42). According to Totton (1965) it has the most complex pattern of branching in the Prayidae. The present specimens differ only slightly from those illustrated by Bigelow (1911).

This is the first record of this species in the Atlantic. Additionally collecting a bract at a depth of 2475 m indicates that at least the eudoxoid is bathypelagic. The polygastric stage is estimated to inhabit a depth of 650-1600 m (Totton 1965). According to Totton (1965) only 16 polygastric specimens have ever been recorded. The paucity of specimens of this and other species may be due to the fact that there has been insufficient sampling of the bathypelagic zone.

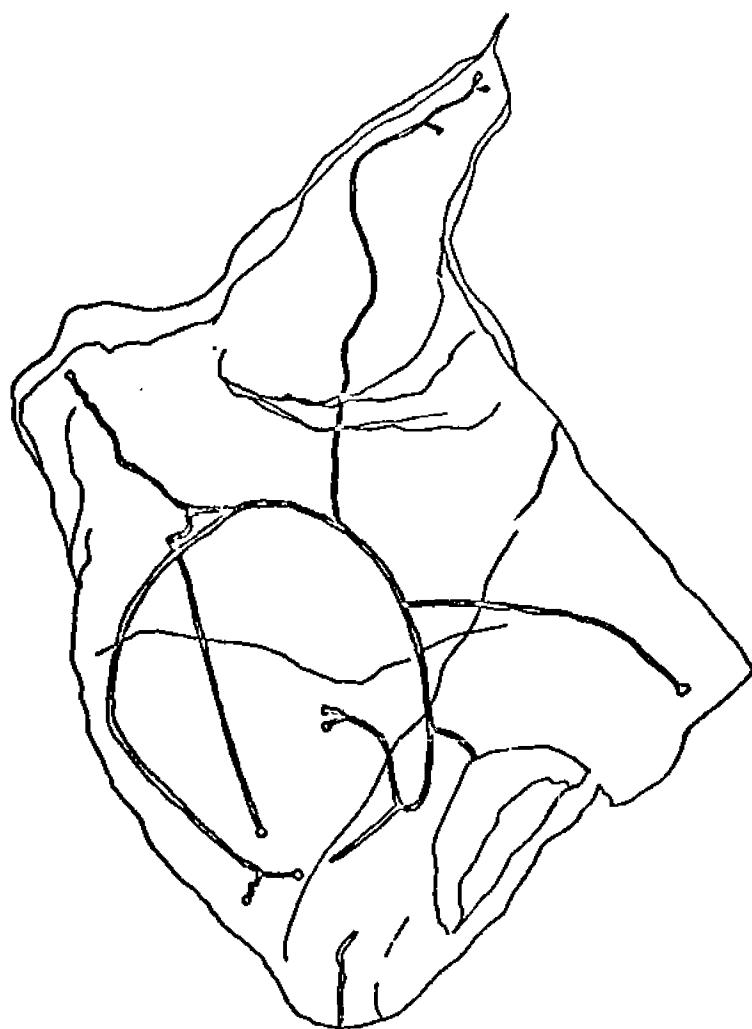


Figure 42. *Nectopyramia diomedae*: Bract (30 mm high). Note complex branching of the phyllocyst (bracteal canal).

Nectopyramis natans (Bigelow 1911)

Material. R/V ALAMOS: Collection 4, 1 bract 26 mm in length

Remarks. As is the case with N. diomedae this is the first record of this species from the Atlantic, all previous records having been from the Pacific. The present specimen was taken from the upper water layers at a depth between 0 and 675 m.

### Pelagic Cnidarian Host-Symbiont Systems

#### Trematoda

Stunkard (1969) worked out the life cycle of Neopechona pyriforme (Linton 1910) (Digenea: Lepocreadiidae) in which medusae (Chrysaora quinquecirrha, Gonionemus vertens and Aurelia aurita) act as atenic hosts, the subadult metacercaria or unencysted metaceracaria being carried as an ectoparasite. Several common teleosts (including sea bass) obtain Neopechona infections by eating infected medusae. Totton (1965) mentions unpublished data regarding infection of physonects with trichocercous cercariae. Dollfus (1963) lists Palearctic and Indian marine Cnidaria which are hosts for digenetic larvae. According to Dollfus (1963) the marine lepocreadiidae have little host specificity.

I have noted on occasion infection of small numbers of Eutima variabilis in Mississippi Sound with a small (1-2 mm) trematode. Unfortunately the specimens were lost in Hurricane Camille before they could be identified. This is the only incidence of trematode infection of Cnidaria in the Gulf that has been reported to date. In the ten infected specimens of Eutima examined there was a maximum of three trematodes per medusa and all trematodes were attached by the anterior sucker to the subumbrellar portion of the bell.

### Cestoda

Stomolonhus meleagris L. Agassiz, the cabbagehead jellyfish, an extremely common coastal rhizostome medusa in the Gulf of Mexico, is commonly infected with an unusual plerocercoid-like larva. This organism, which channels through the tissues of the host, was assigned to the genus Ouwensisia Moestafa and McConaughey 1966. Ouwensisia catostyli M&M 1966 was described from the rhizostome medusa, Catostylus ouwensi M&M 1966 in Irian (Indonesian) waters. Moestafa and McConaughey (1966) examined only five preserved medusae, each heavily infected, particularly near the bell margin and in the oral arms. Ouwensisia n. sp. was studied alive as well as in a preserved state. Observations are included on its behavior and pathological effect. The genus "Ouwensisia" must be considered provisional until the life cycle is resolved in sufficient detail to determine the adult of this worm.

Note is also made of a tetraphyllidean-like plerocercoid from Periphylla periphylla (Peron and Lesueur 1809), a deep water coronate scyphomedusa. The only other report of a tetraphyllidean-like plerocercoid from a cnidarian is that of one taken from the float cavity of the physonectid siphonophore Agalma sp. by Th. Studer (1878) cited by Dollfus (1931, p. 553).

#### Ouwensisia n. sp.

Description. Vermiform, 0.5-4.5 mm in length, circular to ovoid in cross section; color opaque white to translucent depending on the state of contraction and preservation. Cuticle 15-25  $\mu$  thick

and apparently acellular. Deep staining mass surrounding posterior region of cruciform, terminally opening penetration organ (280-500  $\mu$  long). Frontal glands with ducts empty into wall of penetration organ (Figures 43 and 44). Frontal gland cells, 40-65  $\mu$  in diameter, are found throughout length of body (Figures 43-48) but are most abundant in anterior half of the worm, especially immediately behind cruciform penetration organ (Figure 45). Gland cell ducts may extend from the posterior of the organism to anterior deep staining mass. Inner surface of anterior cavity covered with spines, 2-4  $\mu$  in height (Figure 45). An apparent "ventral groove" is visible in the anterior half to one third of the penetration apparatus of some specimens (Figure 48 C). When worms were relaxed by refrigeration or nicotine prior to fixation, about one-third of them everted the penetration apparatus (Figure 48D). Gland cells in posterior half of the animal appear to be arranged in two rows (Figure 43). Osmoregulatory system is present, 4 to 6 flame cells along thin walled lateral ducts (3-5  $\mu$  in diameter) on each side of body. Flame cells demonstrable only in live material. Muscle fibers (including horizontal, oblique and circular elements) scattered throughout body and most numerous anteriorly. Large vacuolar (40-80  $\mu$  diameter) parenchymatous cells dispersed throughout worm. Nervous system not apparent. Photoreceptors absent. Excretory granules or concretions (2-10  $\mu$ ) present and abundantly scattered beneath cuticle (Figures 69 B and C).

Diagnosis. These worms are most probably cestode larvae. The



Figure 43. Owvensia n. sp.: Holotype (whole mount, 4 mm length).  
The anterior penetration organ (upper left) is distinctly  
visible.

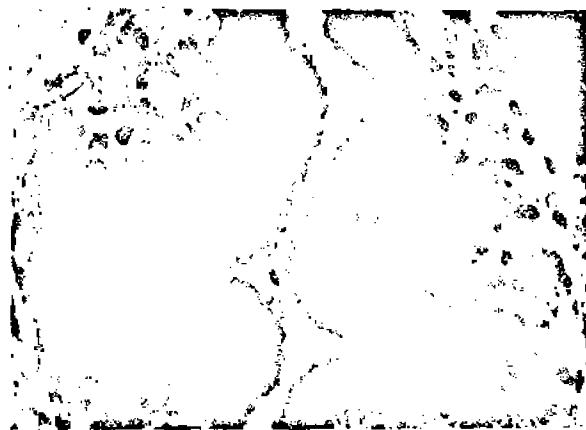


Figure 44. Owvensia n. sp.: X section through cruciform anterior  
penetration organ. Note cuticular teeth (2-4  $\mu$  high).



Figure 45. Ouwensia n. sp.: X section posterior to anterior deep staining mass.



Figure 46. Ouwensia n. sp.: X section through ventral groove region

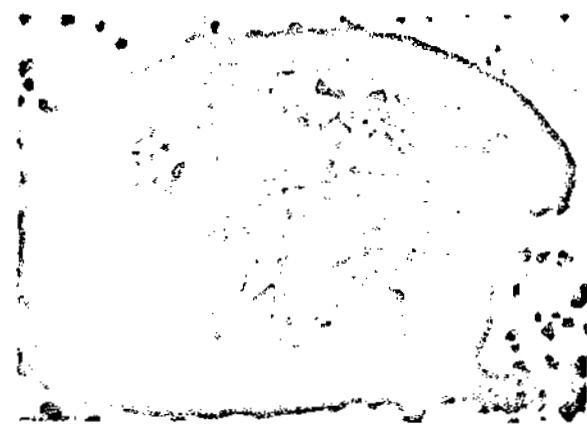
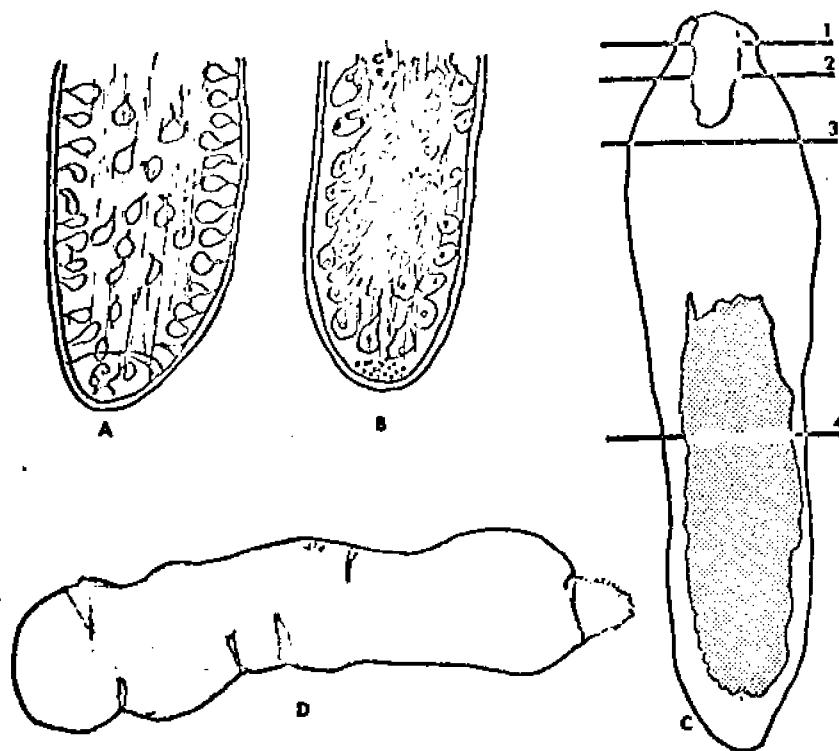


Figure 47. *Ouwensia* n. sp.: X section through posterior one third of body.



**Figure 48.** *Ouwensia* n. sp. and *Ouwensia catostylis* in comparison.  
 A shows posterior region of *O. catostylis* (after Moestafa and McConaughey 1966) showing crescentic groove and terminal pore. B shows posterior region of *O. n. sp.* Note excretory granules and concretions. C shows planes through which sections were taken (1=Figure 46, 2=Figure 44, 3=Figure 45, 4=Figure 47.)

excretory granules are very reminiscent of those described by Wardle and McLeod (1952) for pseudophyllidean larvae. We interpret the large gland cells to be homologous with frontal glands characteristic of other cestode larvae. Mr. Howard Armstrong (Texas A&M Marine Laboratory, Galveston, Texas) found similar if not identical larvae encysted in the intestinal walls of deep sea fishes of the family Macruridae. The identification of these helminths was confirmed by the senior author and Dr. S. H. Hopkins. It is quite possible that the medusa is not the only intermediate host.

O. n. sp. differs from O. catostyli by the absence of a characteristic cap like posterior end marked off by a crescentic groove (Figure 48 A and B). O. n. sp. lacks both the distinctly defined posterior terminal pore (Figure 48) and the orange pigmentation around the anterior "buccal mass" that M&M described for O. catostyli. The anterior "eye" is of dubious significance, as it was found only in a single specimen and (B. H. McConaughey, personal communication), "its true nature can only be guessed at". Moestafa and McConaughey n. sp. did not mention the excretory system, probably because it was not observed in their material which was preserved. The internal arrangement of O. n. sp. is illustrated in a series of photomicrographs (Figures 44-47). The planes through which they were taken are indicated in Figure 48C. The "mouth" (as M&M refer to it) does appear to function as an organ of ingestion, as evidenced

and burrowing as can be observed in the live animal. This is most probably the method used by the worm to move through the host tissue. The use of the lysed host tissue as a nutrient source cannot at this time be definitely claimed. Furthermore, elucidation of the homology of the frontal glands and the anterior funnel with any type of oral structure must await more detailed ontogenetic studies.

Pathology and Behavior. *Stomolophus*, from all localities (Mississippi, Louisiana and Texas) examined to date, when larger than 30 mm in diameter, was commonly infected with Ouwensis. The larvae were present in greatest numbers in the peripheral mesoglea of the bell and oral arms. The short channels produced by the worms are easily seen and are identical with those described by MGM for cystostyli. The number of helminths per individual ranged from 11 to 150+, the larger medusae having the greater parasite burden. *O. n. sp.* is most easily demonstrated in the lappet region where the host tissues are thinnest.

A small percentage of *O. n. sp.* project their anterior ends out through a small pore to the exterior. This has also been noted by Moestafa and McConaughey (1966) for their species. Specimens of cabbageheads have been found where the worms had left the host and a secondary bacterial infection was present in the vacant channels. In heavily infected medusae the larvae form tangled clumps containing as many as 10 organisms each. In and around the lappets are found locally inflamed lesions or

hollow "pits" which occasionally are infected by bacteria and become distinctly necrotic. These lesions are small and apparently not of major consequence to the cnidarian, except possibly in very severe infections. Effects of this parasite on the longevity and population dynamics of the jellyfish are unknown. These events should be investigated because of the great abundance of Stomolophus on the Gulf coast and the significance of this medusa in the estuarine trophic structure (Phillips *et al.* 1969) especially as it relates to commensal juvenile carangids and other teleostean and crustacean predators.

O. n. sp. is easily maintained in the laboratory, surviving up to three weeks in host tissue providing desiccation does not occur. Stomolophus, after being stranded on the beach in excess of 48 hours during midsummer, still retained viable helminth larvae. The worms are best maintained in host tissues under refrigeration between 4-16 C. They become markedly active at temperatures above 20 C. The larvae may also be kept at similar temperatures in sea water of salinities ranging from 10 o/oo to 37 o/oo or in Tyrode's solution for two weeks or more at temperatures of 16 C or lower. These worms are extremely hardy and can evidently withstand considerable environmental extremes. Owensia can also be maintained in sea water agar which they will penetrate in the same way it invades host tissue.

When mechanically removed from host tissue these worms will actively invade any suitable gelatinous substrate. Burrowing is

rapid; at 16°C a 4 mm worm will penetrate 6 mm into a block of medusan tissue in 10 minutes. It channels at about the same rate in sea water agar (16 o/oo) and has been maintained for as long as eight days in this medium at 16°C. The agar medium is evidently not the preferred one since the larvae will periodically leave it (1-48 hours), initiate searching behavior and re-enter within 24 hours. When allowed to channel into medusan pieces no worms were observed leaving the tissue. When in excess of 30 worms were presented with two comparable blocks of agar and host tissue in the same embryo dish (sea water concentration 22 o/oo at 16°C) about equal numbers attacked and began penetrating both the agar and jellyfish fragments. By the next day only 4 worms were burrowed in the agar, 5 were initiating channels into the medusan tissue, 6 were free in the sea water and the remainder had entered into the medusan tissue. Invasion is probably activated by contact with a substrate of suitable consistency.

Burrowing movements are pseudophyllidean-like (S. H. Hopkins, personal communication) involving anteriorly initiated peristaltic waves as well as eversion, grasping and apparent ingestion with the cruciform anterior penetration organ. The worm has been observed to take host tissue into the anterior cavity, and the eversion and retraction of the anterior cavity (or "mouth") are easily seen. Behaviorally as well as morphologically these worms are plerocercoid-like.

Zoogeography. B. N. McConaughey (1970) states that the

of this parasite in the Gulf of Mexico is of distinct zoogeographic significance. He wrote (1970, p. 69) that "this may indicate great antiquity for these worms and the jellyfish hosts, perhaps going back to the Mesozoic era when an uninterrupted, tropical marine biota extended by way of the Tethys Sea from the Indo-Pacific to what is now the Gulf and Caribbean region." Since Stomolophus meleagris also occurs on the Pacific coast of North, Central and South America and the genus Catostylus has a wide Indo-Pacific distribution it would be of interest to examine specimens from these areas for Ouwensisia. Additionally S. meleagris is found as far north as the lower Chesapeake Bay (Pearson 1941) and none from that area have been examined for vermiform parasites. We further suggest the possibility that fishes of the genera Caranx, Peprius, Poronotus and Chloroscombus that commonly associate with Stomolophus (Phillips et al. 1969) may serve as intermediate or transfer hosts for the same worm. Data are unavailable on the associative fishes of Catostylus; however, it is very likely that rhizostomes in the Indo-Pacific have an analogous complement of predators and commensals. It should also be noted that the Indo-Pacific is apparently the center of rhizostome evolution in that it has the richest and most varied fauna of this type. H. B. Bigelow (1919a) considers the Atlantic and Pacific Stomolophus meleagris, in spite of some apparent morphologic dissimilarities, to be conspecific. The two populations probably became distinct when Central America became a geographic barrier.

in the Pliocene. Thus, the occurrence of Ouwensia in Pacific coast Stomolophus would be of special zoogeographic interest and would lend further support to McConaughey's thesis.

**A Tetraphyllidean-like Pleroceroid from  
Periphylla periphylla (Peron and Lesueur)**

A tetraphyllidean-like larva (Figure 49), 2 mm long, was recovered from a lappet of the coronate scyphozoan Periphylla periphylla collected in an Isaacs-Kidd 10' midwater trawl at Lat  $24^{\circ}03'$ , Long  $83^{\circ}07'$  in the Gulf of Mexico at a depth somewhere between zero and 675 meters on 3 July 1965. The larva had four phyllidea but was otherwise relatively undifferentiated. Only five Periphylla from the Gulf were available for examination so the exact extent of the relationship, normal or accidental, is unknown. P. periphylla, however, is a common form of panglobal distribution in colder water masses and material from other areas should be examined for parasites. Dollfus (1931) cites a tetraphyllidean-like larva in a siphonophore, and although I have examined several hundred physonectid siphonophores from the Gulf, no other worms of this type were found. Therefore it is likely that Physonectids may be an accidental host.

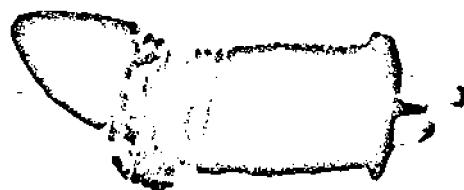


Figure 49. Tetraphyllidean-like larva from Periphylla periphylla.  
Total length is 2 mm.

#### Associative and Symbiotic Crustacea of Cnidaria and Predation

Symbiotic and associative Crustacea found with Gulf estuarine and neritic Cnidaria are discussed in some detail by Phillips *et al.* (1969). Spider crabs (*Libinia dubia*) are commonly taken in association with most scyphomedusae. These spider crabs vary from 4-18 mm in carapace width, and are most commonly found in association with Stomolophus meleagris and Chrysaora quinquecirrha as well as the sea wasp Chiropsalmus quadrumanus. Gutsell (1928) favored the hypothesis that Libinia enters into a transient association when the medusa is near the bottom. This is supported by the fact that spider crabs in the same size range are found associated with sessile hydrozoans and ectoprocts.

The relationship of the spider crab to the medusa is obviously not one of obligate symbiosis. It is more likely a case of predation by the crab. Along the Texas coast (Galveston) on 3 November 1970 I noted two large Aurelia (c.50-70 cm diameter) stranded in the upper portion of the splash zone. One medusa had two small Libinia sp. on its subumbrella obviously feeding on medusan tissues.

As cited by Phillips *et al.* (1969) blue crabs (Callinectes sapidus) are occasionally found in association with sea nettles perched atop the subumbrella. In a previous publication (Phillips *et al.* 1969) I stated that "it is possible that they (the blue crabs) may scavenge on fish the jellyfish has stunned or killed." Since that time I have observed blue crabs to actively feed on sea nettles in the waters of Mississippi Sound.

Additionally, ghost crabs (Ocypode quadrata) scavenge on stranded medusae and beached Physalia. Powell and Gunter (1968) noted that stone crabs (Menippe mercenaria) feed on Stomolophus remains. Hermit crabs also feed on medusan tissue (Phillips et al. 1969).

Hyperiid amphipods (genus unknown) were found in the calyphoran siphonophores, Diphyes dispar, Chelophys appendiculata and Hippopodius hippocampus. Unfortunately all specimens were lost in Hurricane Camille. Less than ten specimens out of several thousand siphonophores harbored these amphipods.

All of the relationships of crustacea and medusae so far discussed are not host specific and, with the exception of the endoparasitic hyperiid amphipods, are primarily transient.

Parasitic isopods (genus unknown) occasionally attach to sea nettles and sea pansies (Renilla mulleri) in northern Gulf waters. Barham and Pickwell (1969) discussed an association between the giant parasitic isopod Aniropus branchiotor with the remarkable scyphozoan Deepstarla enigmatica. Photographs taken by the submersible "Deepstar" show this isopod clinging to the subumbrella surface at time of capture. Barham and Pickwell (1969) stated that the medusa "did not pulsate or show normal swimming movements. Instead the medusa appeared flaccid and seemed to be floating passively." Russell (1967) noted the absence of stomach epithelial lining and parts of the coronal muscle and suggested that the medusa was moribund at time of capture. Taking into account the occurrence of

nematocysts in the stomachs of some anuropods (as reported by Menzies and Dow, 1958, and cited by Barham and Pickwell), Barham and Pickwell suggested that the isopod feeds on the jellyfish, incapacitates medusa movement and creates a "floating protective environment," which they state is a process that stops "somewhat short of the reduction of salps and pyrosomes into thin-walled houses by the well known amphipod, Phronima sedentaria." It should be noted that Barham and Pickwell did not demonstrate nematocysts in stomach content analysis of the associated Anurepus. Whether the isopod may be traveling on an atonic host or is actually a true parasite of Deepstaria is purely conjectural. Additionally there are no criteria for establishing exactly what are the normal swimming movements in Deepstaria. I find it difficult to believe that Anuronus incapacitates the medusa since my own published (Phillips et al. 1969) and unpublished observations indicate that medusae can serve as hosts for a wide variety of crustacea and other metazoans without suffering incapacitation. In actual fact the moribund state will render an organism prey for a wide range of animals which would not ordinarily attack it. Quite possibly this may be the situation with respect to the giant isopod and Deepstaria.

Incidentally, it is exceedingly dubious that Phronima invades salps or pyrosomes and converts them into thin-walled houses as stated by Barham and Pickwell (1969). The structure of the amphipod house bears little resemblance to that of any pyrosome or salp and the limited resemblance at best is highly superficial.

(Dr. Leo Berner, Jr., personal communication). It is much more likely that Phronima secretes its own domicile. Examination of the isopod house evinces no evidence of zooids of any type ever having been embedded in the gelatinous matrix. There is also a very striking correlation between house dimensions and amphipod size with respect to length, diameter and thickness of the gelatinous matrix which would certainly indicate the secretory nature of this gelatinous house.

One specimen of Deepstarria enigmatica taken in the Gulf of Mexico had no crustacean symbionts attached to it and examination of the remainder of the Issacs-Kidd midwater trawl sample revealed no Anuronus. It remains to be determined whether or not life cycle completion in the giant isopod is dependent on a cnidarian host. Data regarding the association between Anuropus and Deepstarria are insufficient for concluding (as do Barham and Pickwell 1969) that a definite host-parasite system exists. Clearly the statement by Barham and Pickwell (1969) that "the long term, internal, symbiotic association between anuropids and Deepstarria enigmatica appears to be quite unique" is a very definite zoological non sequitur.

#### Fish-Jellyfish Coactions

Fish-jellyfish symbioses in Gulf of Mexico waters have been discussed at length by Phillips et al. (1969). Mansueti (1963) gives an exhaustive review of all known fish-jellyfish symbioses and a discussion of symbiotic relationships in Chesapeake Bay. All scyphomedusae in northern Gulf of Mexico waters

or symbiotic fishes. These fishes are primarily juveniles and exhibit little host specificity. Gulf butterfish (Peronotus burti) are clearly predatory on medusae and in Gulf waters are found primarily in association with Cyanea capillata and Stomolophus meleagris. Bumpers (Chloroscombrus chrysurus), harvestfish (Pedilus paru), jacks (Caranx sp.) and triggerfish (Monacanthus hispidus) are commonly found in association with sea nettles, cabbageheads and Cyanea. All of the associative fishes are juveniles (maximum standard length 35 mm). Generally the larger the medusa the greater the number of associative fishes.

The nature of the fish-jellyfish relationships is discussed at great length by Mansueti (1963). Mansueti concluded that fishes in association with scyphomedusae are inquiline, transient associates which exhibit predatory behavior. The same basic pattern applies to northern Gulf fish-jellyfish interactions. Predatory behavior is much more manifest as the fishes increase in size. Amongst known adult predators of medusae are in the Gulf spadefish (Chaetodipterus faber), jacks and bumpers as well as butterfish and harvestfish. Additionally sharks have been reported to feed on medusae (Rae 1967) and I have observed sharks to attack Physalia.

Although Nematus is a common commensal of the Portuguese Man O' War in tropical Gulf waters none were found in association with Physalia in the northern Gulf. S. H. Hopkins (personal communication), however, has observed this association at Port Aransas.

For accounts of immunity of commensal or symbiotic

nematocysts the reader is referred to Phillips et al. (1969) Mansueti (1963) and Dahl (1961). The immunologic aspects of the subject are very poorly known and very confused. Apparently the same species of fish may or may not be immune to host jellyfish nematocysts depending on geographic location and hydrographic factors (temperature and salinity) as well as the physiologic state of the medusa.

#### Parasitic Cnidaria

Parasitic forms are known for all three classes of Cnidaria. In northern Gulf waters an undescribed anemone is found in the radial canals of the rhizostome medusa Rhopilema verrilli. These anemones have very reduced tentacles and are flattened in either a dorso-ventral or lateral plane. These parasitic anemones are 3-4 mm in maximum dimension. No other parasitic anthozoa are known from the Gulf of Mexico. The life cycle of this curious anemone is entirely unknown.

In the Hydrozoa several larval types may be interpreted to be parasitic. In the present study narcomedusan larvae are commonly found attached to subumbrial regions of the hydromedusae Rhopalonema velatum and Bougainvillia platygaster. Kramp (1959) refers to narcomedusan larvae as commensals. Kramp (1957 and 1959) discusses the occurrence of narcomedusan larvae on B. platygaster, Rhopalonema velatum and Rh. funeralium. In the present study 8 out of 40 B. platygaster had clusters of narcomedusan larvae attached to manubrium. These larvae are apparently identical to those found

by Kramp (1957 and 1959) which he identifies tentatively to be of Pegantha trifolia.

Parasitic narcomedusan larvae attached to Rhopalonema velatum are usually small and actinula-like, without proliferative stolons, and are attached to the subumbrial surface. Approximately 1 percent of the 800 Rhopalonema velatum taken by the R/V ALAMINOS were infected. The host medusae did not appear to be at all degenerated. Kramp (1959) however, states that the hosts are "more or less degenerated, destitute of gonads and usually without a manubrium" (in reference to Rhopalonema velatum). Since this degenerate medusa was not encountered in this study it may be likely that the larvae observed by Kramp were of a different species of narcomedusan than those infecting Gulf of Mexico trachymedusae. The two specimens of the bathypelagic Rhopalonema funeralium taken in the Gulf had no parasitic narcomedusan larvae.

Of narcomedusae taken in the Gulf all, with exception of Solmundella bitentaculata and Aegina citrea, were observed to have developing larvae attached to the walls of the gonads, stomach pouches or canals. These "parasitic" larvae are released from a proliferative bud or gonad and attach to other tissues of the maternal medusa. In essence these narcomedusae may be considered viviparous. A number of anthomedusae (Bougainvillia platygaster, Sarsia prolifera, Cyanea tetrastyle) and the limnomedusan Proboscidactyla eremicus produce medusa buds or proliferative stolons which release juvenile medusae, thus bypassing the alternate sessile hydroid stage.

medusa larvae are produced in situ in the parent medusa.

In Gulf of Mexico Scyphozoa the closest condition approximating the condition found in hydromedusae is the release of well developed planulae by Cyanea capillata and Pelagia noctiluca. Pelagic noctiluca is the only member of the Pelagiidae to lack a sessile scyphistoma; the planulae of this species develop directly into ephyrae.

In the Scyphozoa the closest condition to larval parasitism is that of the larva-parent relationship of the deep water, viviparous medusa Stygiomedusa fabulosa (Russell and Rees 1960) wherein the planula attaches and embeds in the stomach pouches of the parent, producing a "parasitic" strobila which releases juvenile medusae (i.e. meta-and post-ephyral stages). Russell and Rees (1960) state this condition is an adaptation to a bathypelagic oceanic habitat where suitable substrates for strobila development are absent or the probability of the planula finding a suitable substrate is infinitesimal. As interpreted by Russell and Rees viviparity is common amongst oceanic invertebrates due to the lack of shallow substrates available to neritic relatives.

#### Ecologic Significance of Cnidarian Hosts, Parasites and Symbionts

In general, Gulf of Mexico Cnidaria are of minor significance as metazoan parasites in these waters. Other than ectocommensal hydroids and anemones occasionally found in association with crabs there are no other parasitic or symbiotic cnidaria found in association with higher metazoans in the Gulf of Mexico. The only record of Proboscidactyla ornata (given the name Lyr) is from the

be symbiotic on sabellid worm tubes (Mayer 1910). Strickland (1971) reported that the migrating stolen of the Pacific Proboscidactyle flavicirrata differentiates only upon contact with a suitable worm. Strickland thought that an inducer substance produced by the worm may be involved. There have been, however, no studies of the physiological basis for the host specificity and mode of induction in symbiotic or parasitic Cnidaria.

There are no data for effects of parasitic narcomedusae on population dynamics of host medusae. Patchiness in oceanic distribution of host medusae may be related, at least in part, to population reduction as a result of narcomedusan larval parasitism.

Pelagic cnidaria act as transport hosts of lepocreadiid trematodes and possibly of various cestodes and parasitic isopods. This is the major significance of their symbiotic relationship.

The effects of protozoan and vermiform parasites on medusa population levels is entirely unknown and should indeed be investigated as a potential method of biological control of noxious forms in select coastal areas where local populations of sea nettles and sea wasps create distinct hazards. In view of recent research efforts toward devising control measures for noxious coastal medusae (Cargo and Schultz 1966 and 1967) it seems that intensive study of bacterial, protozoan and metazoan parasites of medusae may have significant application and offer excellent research potential in evaluating factors responsible for yearly fluctuations in populations of coastal medusae.

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## ZOOGEOGRAPHIC CONCLUSIONS

New records of medusae and siphonophores for the western Atlantic other than new species are given in Table 31. Of the new species described one, Koellikerina n. sp., is most closely related to the east Atlantic K. fasciculata. Halistaura, a genus previously only known from the Pacific, is reported herein from the Atlantic. As previously discussed Zancleopsis n. sp. is most probably of Pacific origin. The presence of such Pacific medusae as Rythotira depressa and Calycopsis simulans in the Gulf of Mexico and in scattered Pacific localities is most easily explained by assuming an Indo-Pacific origin and a Tethyan connection between the western Atlantic and Indo-Pacific. The recent studies by Kramp (1970) on the zoogeography of rhizostome medusae certainly supports the Indo-Pacific origin hypothesis.

In discussing the discontinuous distributions of carideans found in the Indo-Pacific and the Gulf of Mexico, Pequegnat (1970) favors the explanation that "lack of adequate sampling in all areas of the deep sea is the reason for the apparent discontinuous distributions." Although this may be true up to a point, the Indo-Pacific origin of the cnidarian fauna seems indisputable and is also supported by the occurrence of the cestode-like parasite Ouwensia n. sp. in Stomolophus. The zoogeographic implications of this parasite have been discussed in the previous section.

The occurrence of forms previously known from the Indo-Pacific in the Gulf of Mexico (Table 31) most certainly

stretching from the Caribbean to the Mediterranean to the Indo-Pacific and is undoubtedly a result of dispersion via the Tethys Sea and/or communication across Central America before the Pliocene.

As demonstrated by the present study the Gulf of Mexico is divisible into two distinct faunal zones (Figure 12): (1) a northern neritic Carolinian fauna which is most probably a Pleistocene relict (as indicated by discussions regarding the distinctness of such medusae as Cyanea, Chrysaora and Aurelia in the Gulf) and (2) a southern West-Indian tropical fauna with distinct Pacific faunal elements, found nowhere else in the western Atlantic. The occurrence of such leptolinids as Zygocanna vagans, Orchistoma pileum and Bougainvillia platygaster in the epipelagic waters of the Gulf of Mexico is most certainly indicative of a southern Gulf neritic origin. Quantitative morphologic characterization of intraspecific populations as demonstrated in Bougainvillia carolinensis can be related to geographic isolation and if one has sufficient patience can be used to define water masses.

In addition to the two faunal assemblages just discussed the bathypelagic fauna of the Gulf is of considerable significance. The shallow sill depths at the Yucatan and Florida straits (2000 m and 800 m respectively) might well be a formidable barrier to many bathypelagic forms; however, the bathypelagic forms considered in this report (Periphylla periphylla, Periphyllopsis braueri, Rhopalonema funerarium, Halicreas minimum, Crossota rufa, Pantachefon heckeli, Erenna richardii and Aeginura gracilis)

known to occur in upper water strata during periods of upwelling and could easily traverse these relatively shallow sill depths with cold water currents. The deep water circulation of the Gulf of Mexico is so poorly known at the present time that no more can be said about its effect on the bathypelagic Cnidaria of the Gulf.

This study of the pelagic cnidaria in the Gulf of Mexico indicates that many leptolinid members of the fauna would be excellent indicators of neritic discharge into the Gulf and that abundance of calycophoran siphonophores in coastal areas can give an excellent quantitative index of mixture of neritic, estuarine and oceanic waters.

The major conclusion to be drawn from this study is that, with respect to the pelagic cnidaria, the Gulf of Mexico is a zoogeographically distinct faunal zone in the western Atlantic having common ties with the Carolinian, West Indian, East Atlantic and Indo-Pacific faunae. This fauna results from the Pleistocene isolation of the Northern Gulf, from the dispersion from the Indo-Pacific made possible by the submergence of Central America before the Pliocene, and from survival of remnants of a widespread Tethys Sea fauna.

TABLE 31  
FIRST RECORDS OF PELAGIC CNIDARIA FOR THE WESTERN ATLANTIC  
OTHER THAN NEW SPECIES

	Previously known from	
	East Atlantic	Pacific
<b>Anthomedusae</b>		
<i>Euthotiara depressa</i>		X
<i>Calycopsis simulans</i>		X
<i>Dipurena ophiogaster</i>	X	
<i>Sarsia gemmifera</i>	X	
<i>Stenstrupia nutans</i>	X	
<b>Leptomedusae</b>		
<i>Zygocanna vagans</i>	X	
<b>Siphonophora</b>		
<i>Amphicarpon peltacea</i>		X
<i>A. ernestii</i>		X
<i>Clausophyes ovata</i>		X
<i>Marescursia praeclarus</i>		X
<i>Marrus orthocannoides</i>		X
<i>Nectopyramis diomedae</i>		X
<i>Nectopyramis natans</i>		X
<i>Praya dubia</i>		X
<b>Scyphozoa</b>		
<i>Atolla vanhooffeni</i>	X	
<i>Deepstaria enigmatica</i>		X
<i>Periphyllopsis braueri</i>		X

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