The Classification and Distribution of the Class Scyphozoa

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Introduction

The class scyphozoa is approximately made up of 4 orders, 2 suborders, 24 families, 11 subfamilies, 71 genera and over 220 species. Members from this class, commonly referred to as jellyfish, inhabit all the oceans and seas of the world, from the tropics to the Arctic and Antarctic. The majority of the species live in shallow coastal waters, though there are species have been found in deep seas. Regardless of the extensive distribution and varied diversity, there is relatively little known about these animals. Much of what we know about scyphozoans is due to our occasional inability to coexist with the creatures. The "bloom" that occurred in the early 1980's in the Mediterranean, which greatly affected tourism in the area, generated much of our new knowledge about the jellyfish (Arai, 1997). Fishermen regret happening upon swarms that clog their nets and swimmers run from the water after being stung. In the past, scientists would drag nets at varying depths around the sea and observe what was caught and describe the bottled species at a later date. We now have the ability to enter their pelagic world by scuba and deep sea submersibles. Even though our methods have advanced, there remains much to be discovered about these eyeless and brainless creatures.

This paper will present an overview of the class Scyphozoa, beginning with the Phylum Cnidaria and the placement of Scyphozoa in the phylum, then their natural history, life cycle and physiology will be discussed. Lastly, the diversity of Scyphozoa will be examined by explaining various morphological features found in the different families — features that have made them better suited to exist in the environments in which they inhabit.

The Phylum Cnidaria

There are four classes of Cnidaria, they are are: Anthozoa, Scyphozoa, Hydrozoa and Cubozoa (Chart 1). Cnidarians are diploblastic consisting of the endoderm (sometimes referred to as the gastrodermis) and the ectoderm (the epidermis). Between the two cell layers is the mesoglea, which ranges from little more than a glue that binds the layers (in most Hydra) to the vast bulk of the animal (Class Scyphozoa). The body encompasses a single sac-like body space, the coelenteron, which is in contact with the surrounding water through the mouth. The less preferred name of the phylum, Coelenterata, is based on this attribute. The coelenteron (also termed the gastrovascular cavity) serves for gas exchange and digestion.

All cnidarians are carnivorous, with the cnidae, or the stinging organ, on the tentacles active in prey capture (Figure 1). Polyps are typically sessile cnidarians and are generally believed to be passive predators, feeding on prey items that blunder into their tentacles. However, some cnidarian medusae possess sensory structures, like the primitive eye (Figure 2) found in the Cubozoa (Pearse and Pearse 1978). Some cnidarians can absorb dissolved organic matter directly from seawater (Schlichter 1975), but it is not known how widespread this ability is. Living within the tissues of many species of anthozoans, hydrozoans and a few species of scyphozoans, is a unicellular alga from which the animals derive reduced carbon (Shick 1991). Dinoflagellate symbionts, by far the most common algal symbionts, are found in cnidarians. Zoochlorellae or green algal symbionts, occur in both marine and freshwater cnidarians.

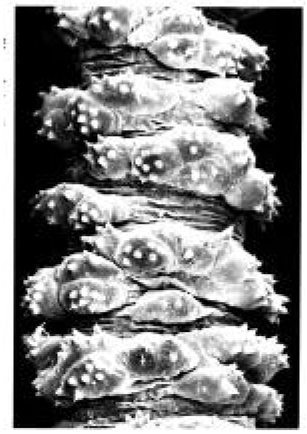


Figure 1. SEM of cnidae on a tentacle.

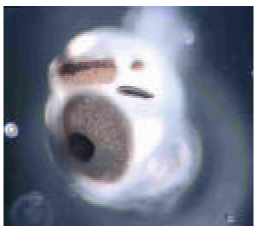


Figure 2. The primative eye of the Cubozoa.

Cnidarians have hydrostatic skeletons, regardless of whether they also have mineral and/or organic exoskeletons or endoskeletons. Members of this structurally simple marine phylum possess one of two body forms. The muscles of the body wall operate against the fluid in the coelenteron to extend individual polyps and produce the swimming effect of the medusae. The hollow tentacles of anthozoans are extended through hydrostatic action as well. Sea anemones, sea whips, corals and hydroids are all polyps growing attached to rocks or other hard surfaces of the sea. A major group of the cnidarians, the Anthozoans, has no medusae stage as it has been assumed to have been lost (Hyman 1940).

Phylogenetic Relationships

The exclusively aquatic phylum Cnidaria is represented by polyps such as sea anemones and corals, and by medusae such as jellyfish. A polypoid or a medusoid Cnidarian is a radially or biradially symmetrical, uncephalized animal with a single body opening, the mouth. The mouth is surrounded by tentacles studded with microscopic stinging capsules known as nematocysts that are the means of both offense and defense. The possession of nematocysts, or stinging cells, is the defining characteristic of the phylum (Hessinger and Lenhoff 1988).

Along with Porifera and Ctenopora, the Cnidaria are animals that could be one of the first offshoots of the metazoan phylogenic tree (Ax 1989). There are two hypothesis for the origin of the stem line of Cnidaria. The first theory, the "Basal Trachymedusae" hypothesis, held by many Americans scientists, suggests that a holoplanktic medusae-like stage gave rise to all known cnidarians by introducing a sessile polyp stage (Hyman 1940). The opposing view, the "Medusozoa" hypothesis (Figure 3) held mostly by European scientists, assumes that only the polyp stage was present in the stem species of Cnidaria (Bouillon 1981). Due to parsimony and the fact that there is a polyp stage in all four cnidarian classes, it is assumed that a single, deep sea polyp stage was also present in the first stem species of Cnidaria. Because of its occurrence in all Cnidaria, the polyp must have also had a planula larva as a distributive unit. The debate between the American scientists and their Europeans colleagues originates in whether or not the cnidarian stem had a medusae stage (Schuchert, 1993).

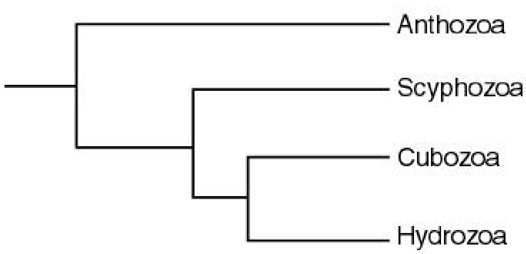


Figure 3. Evolutionary relationships of the Cnidaria, after Bouillon (1981).

Cnidarians have several similarities with their closest relatives the Ctenophora. The Ctenophora are epithelial in organization, lack any excretory organs, have planktonic occurrences, and a gelatinous body. However, they differ in that the cnidarian medusae have a concave subumbrella and swim by means of jet propulsion. Furthermore, the Ctenophores are bisymmetric and rely on cilia for movement.

RNA analysis has shown an association between the two phyla (Bridge et al, 1995). Because of this close relationship, it is now assumed that Cnidarians evolved from a planktonic stage. When Bridge, et al (1995) considered molecular and morphological data, the Medusoza hypothesis was supported (Figure 3). Neither of these theories attempts to include the extinct class Conulata, which has been considered by most paleontologists to be related to the Scyphozoa (Bridge, 1995). Few molecular phylogenetic analyses so far have examined the Cnidaria in great detail.

Commonly known members of Cnidaria, neither of which is considered a "true jellyfish" are the Portuguese Man-of-War (*Physalia physalis*) and the Sea Wasp (*Chiropsalmus quadrumanus*). Although a member of the phylum Cnidaria, the Portuguese man-of-war is not a "true jellyfish." These animals consist of a complex colony of individual members, including a float, modified feeding polyps and reproductive medusae. Though pain from its sting may be accompanied by headaches, shock, collapse, faintness, hysteria, chills, fever, nausea and vomiting, this cnidarian is not the most harmful to humans. The Sea Wasp known as the Box Jelly because of its cube-shaped bell, is one of the most venomous of the pseudo-jellyfish. Their potent sting can cause severe dermatitis and may even require hospitalization for humans. Sea wasps are strong, graceful swimmers reaching 150 mm in diameter and in height. Several long tentacles hang from the four corners of the cube. A similar species, the four-tentacled *Tamoya haplonema*, occurs along the east coast of the United States. *Chironex fleckeri* is a small tropical Cubomedusea and has been responsible for over 50 fatalities along the Australian coast. The toxins are so potent to humans that death can occur in three to twenty minutes after the sting (Arai, 1997).

Natural history

Cnidaria is thought to have one of the longest fossil histories of metazoan phyla with representatives in the Ediacaran fauna of the late Precambrian . These earliest fossils are both medusoid and polypoid, and thought to represent all cnidarian classes (Scrutton, 1979). Despite this, Cnidarians present particular problems for systematists. Their comparatively simple morphology makes it difficult to compare taxa. The fossil record of soft-bodied cnidarians is very sparse, although the record of corals and other mineralizing cnidarians is excellent.

Cnidarians possessing hard skeletons, in particular the corals, have left a significant legacy of their existence. While a few mineralized coral-like fossils have turned up in the Cambrian Period, identifiable corals began an evolutionary radiation in the Early Ordovician. All these forms were wiped out at the end of the Permian Period, in a mass extinction event that claimed close to 95% of all marine invertebrate species (Robon, 1985).

Class Scyphozoa

Few marine creatures are as mysterious as the scyphozoans, referred to here as "true jellyfish" and include most of the jellyfish familiar to beach-goers. Though easily recognized, this animal is often misunderstood by bathers and beachcombers who react with fear upon encountering this creature. When a human is stung, the victim may experience skin rashes, muscle cramps, or even death. [A report (Mayer, 1910) from Dr. Edward Old, U.S. Navy, 1906: "The stings of *Lobonema* can be quite painful. Soon general pains develop throughout the body, especially the lumbar region. The patient becomes hysterical, coughs incessantly and is nauseated. The pulse becomes rapid and a fever develops. The symptoms develop from 10 to 15 minutes after the sting. One of these cases proved to be fatal."]. Jellyfish inhabit every major oceanic region of the world and are capable of withstanding a wide range of salinity and temperature. Most jellyfish live in shallow coastal waters, but a few species inhabit depths of 4600 meters (2000 fathoms, 1 fathom = 1.8 meters). In northern waters, large groups of jellyfish several kilometers long sometimes hamper fishing by clogging nets (Arai, 1997).

Jellyfish range in size from a mere twelve millimeters to more than two meters across, the largest is *Cyanea arctica*, which may have tentacles over 40 meters long (Meyer, 1910). Despite their often enormous size, jellyfish have no head, no skeleton, and no special organs for respiration or excretion. Their life cycle involves an alternation between sessile polyp phase and a free-swimming medusae stage, though the medusae stage, shown in Figure 4 usually predominates (Arai, 1997).

Physiology

Scyphozoans lack brains, eyes, ears, gills, and heart; the structures that they do possess are usually found in multiples of four (Arai, 1997). Two thin layers of cells, an outer layer (ectoderm) and an inner layer (endoderm) filled with a jelly-like substance called mesoglea make up their bodies (Figure 4). The mesoglea layer of the scyphozoa is very thick with the consistency of firm gelatin. For this reason the class has been given the name "jellyfish." Jellyfish have a simple digestive cavity (coelenteron) which acts as a gullet, stomach and intestine with one opening for the mouth and anus. There are four to eight oral arms are located near the mouth and are used to transport food that has been captured by the tentacles. Jellyfish occur in a wide variety of sizes, shapes and colors. They are 97 percent water and are semi-transparent or glassy and bell-shaped. Regardless of their size or shape, most jellyfish are very fragile, often containing less than 5% solid organic matter (Arai,1997).

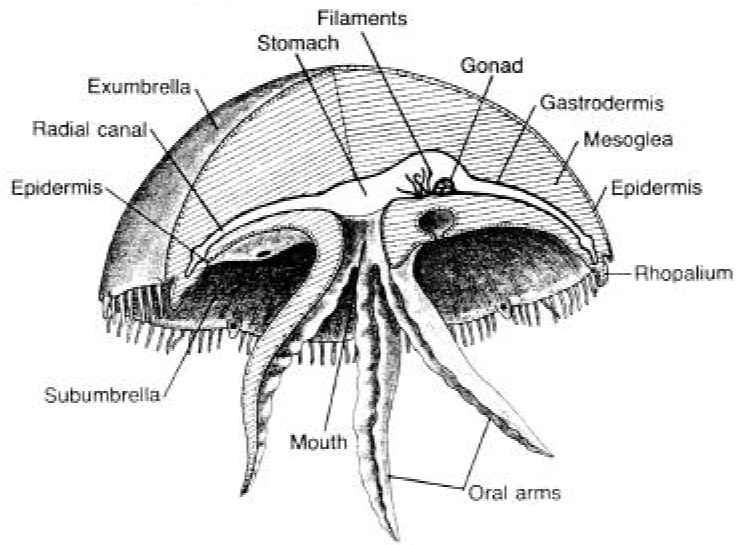


Figure 4. Cross section of a common jellyfish.

The inverted bell-shaped morphology of many of the species that make up this class is referred to as "medusiod." This inverted bell usually has tentacles extending downward from the medusae body. The mouth of the Scyphozoa is at the end of a cylinder that is known as the manubrium (Figure 4). Most scyphozoan species are capable of swimming by use of the muscular mesoglea. The nervous system is of the nerve-net type and is synaptic. Nerve rings occur only in the Coronatae (and Cubomedusae in the Cnidarian phylum). The pulsation control is centered on marginal concentrations of neurons.

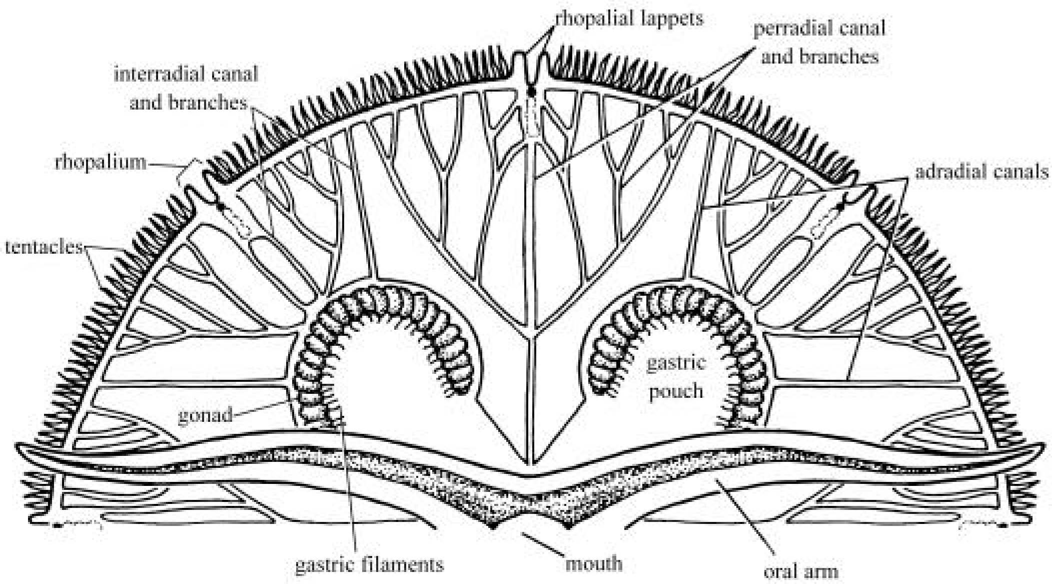


Figure 5. Horizontal cross section of a simple scyphozoan medusa.

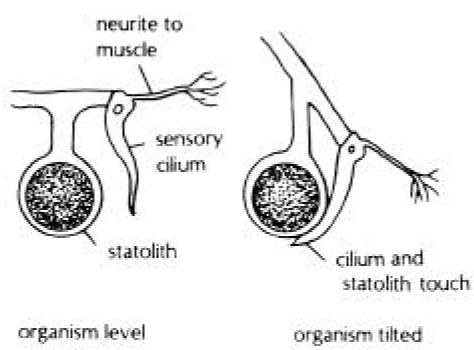


Figure 6. The rhopalia.

Instead of a brain, true jellyfish possess an elementary nervous system, which consists of receptors capable of detecting light, odor and other stimuli and coordinating appropriate responses (Hamner, 1995). Scyphozoans have very efficient sensory receptors. They have a balance organ called a statocyst, simple light detectors called ocelli and some species have touch receptors called sensory lappets. These simple organs are distributed around the margins in club-shaped structures called rhopalia (Figure 6). The rhopalia hang freely around the bell at the margin. Each of the rhopalia is next to sensory cilia. If the animal tilts in a particular direction, the statocysts press against the cilia, causing the nerve cells to generate their action potentials. This system provides a mechanism through which the animal can become informed of its orientation and can alter its posture by stronger contractions on one side of the bell (Arai, 1997).

Life Cycle

The jellyfish's life cycle is what truly distinguishes it. True jellyfish have two distinct body forms, medusae and polyp, reproduce both sexually and asexually, and go through five life stages: egg, planula, polyp, ephyra and medusae. Parental care in the class Scyphozoa is not known to occur.

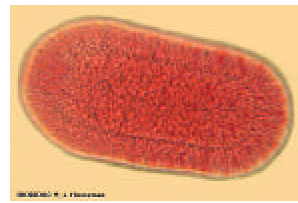


Figure 7. The planula.

The life cycle (Figure 8) of a typical jellyfish involves an alteration of generations in which the animal passes through two different body forms. The dominant and conspicuous medusae is the familiar form, while the smaller polyp form is restricted to the larval stage. Jellyfish are either male or female and reproduce sexually. The reproductive organs (gonads) develop in the lining of the gut. During reproduction, the male releases sperm through its mouth into the water column. The sperm swims into the mouth of the female where fertilization occurs. Early embryonic development begins either inside the female or in brood pouches along the oral arms. Small swimming larvae (planula) leave the mouth or brood pouches and enter the water column (Figure 7). The larvae then seek a shaded surface and attach to the bottom, forming polyps. Polyps of some species propagate vegetatively, forming colonies (if the progeny remain attached to one another) or clones (if the progeny separate). The polyp form resembles a flower, with the bottom of its stalk attached to a stable surface. The tentacles and oral arms facing upward. A polyp can live for several years, producing clone polyps by budding, and eventually beginning a process called

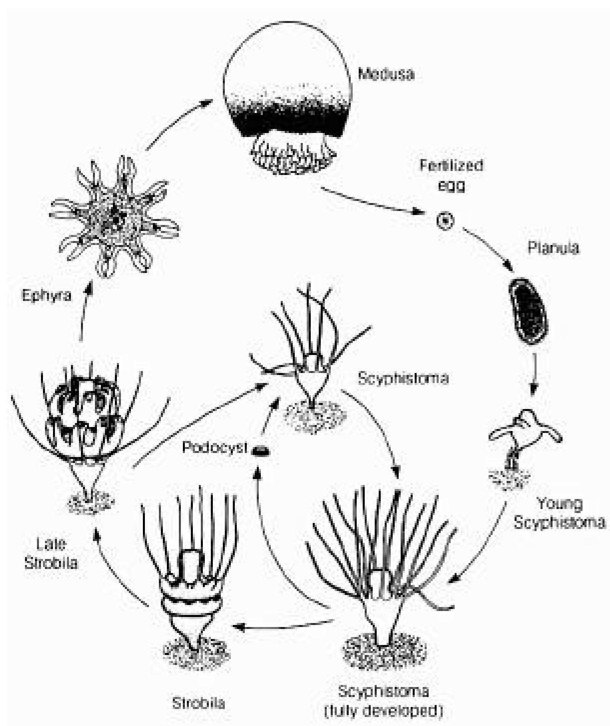


Figure 8. Graphic detailing the life cycle of true jellyfish

strobilization that will transform a single polyp into several organisms (Ruppert, 1994). Strobilization is the asexual reproduction process. When strobilization begins, horizontal grooves appear along the length of the polyp. The grooves deepen until the polyp is transformed into a column of multiple organisms. These organisms, stacked one on top of the other like a stack of pancakes, pop off the top of the column and become free-swimming, immature medusae called ephyra (Figure 8).

When the ephyra first breaks off the polyp, the bell is star-shaped with eight or more points. As the ephyra grows, these points grow together until the animal assumes the adult medusae form and the process starts over again. In a few weeks, an ephyra will grow into an adult medusa, thus completing the complex life cycle. Jellyfish normally live three to six months.

Some scyphozoan species such as Pelagia, Atolla and Periphylla avoid the necessity of the substratum by producing one adult from a single egg. In Chrysaora and Cyanea the larva are retained on the parent in cysts. In Stygiomedusa, the deep-sea medusae, the cysts are highly specialized and the scyphistomae occur in the gastric brood chambers (Arai, 1997).

Locomotion

The adult medusa jellyfish drifts in the water with limited control over its movements. When the animal contracts its circular and radial muscles, the volume of water enclosed under the bell decreases propelling the animal. The net forward movement of the animal occurs primarily because the speed with which the bell contracts exceeds that speed with which the bell recoils to its resting state (Pechenic, 1995). This pulsating rhythm allows for some regulation of vertical movement. Because scyphomedusae are sensitive to light, this vertical movement can be important. Some jellyfish, like the (*Aurellia*), descend to deeper waters during the bright sun of the midday and surface during early morning, late afternoon and evenings (Hamner, 1995). Despite this ability to move vertically, jellyfish depend upon ocean currents, tides and wind for horizontal movement. It is the world wide ocean currents that are responsible for the successful distribution of scyphozoans.

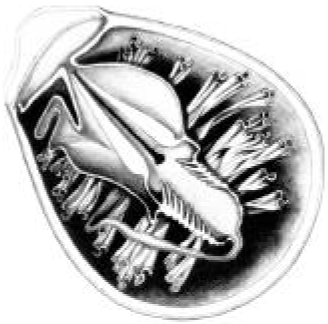


Figure 9. An example of a cnidocyte before its triggered.

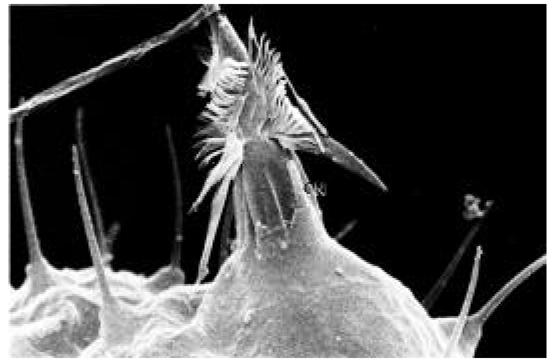


Figure 10. SEM of a nematocyst after release. Note triggers in background of other nematocysts.

Nematocysts & Feeding Mechanisms

Perhaps the most characteristic structure of Cnidaria is the stinging organelle called the nematocyst (Figures 9& 10). Over 20 different types have been described so far and are important in taxonomic determinations. Nematocysts are the most diverse and widespread of three types of cnidae (cnidos = thread, from which the phylum derives its name). The nematocyst is enclosed within a cell called the cnidocyte, which in most instances bears a trigger-like cnidocil which is a modified cilium. Some scyphozoans have relatively powerful nematocysts and many jellyfish make use of them to feed on small fish or crustaceans. Another jellyfish, *Aurelia*, is a flagella-mucus feeder. Small animals and plankton are caught on its tentacles which are then "licked off" the lappets by the oral arms (Figure 21). Currents produced by the flagella in the grooves on the oral arms carry the particles into the stomach (Costello and Colin, 1995).

Scyphozoans are passive but very efficient predators and do not actively search for prey. Instead of actively searching for prey, they drift in currents, pulsing their way up and down the water column, capturing mostly herbivorous zooplankton that happen upon their tentacles (Arai, 1997). Any animal drifting into reach of a jellyfish's tentacles or oral arms activates the stinging cells causing nematocyst to fire and deliver a toxin that stuns or kills the animal. Using its oral arms and tentacles, the jellyfish then “rolls” the food up the tentacle and into its mouth. The mouth opening lies in the center of the underside of the umbrella and leads straight into the gut. This is where the food goes in and the waste comes out.

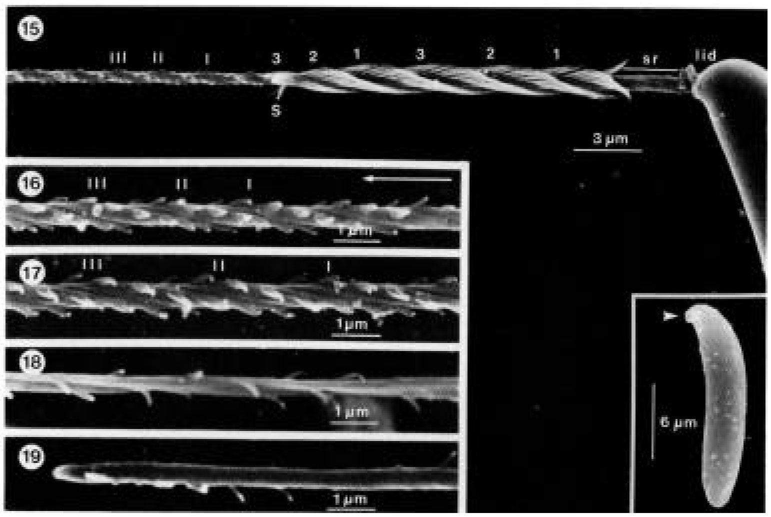


Figure 11. SEM of discharged nematocyst tubules.

There are three major types of cnidae: spirocysts, ptychocysts and nematocysts. Spirocysts, which are adhesive in nature, are found only in Anthozoa. Ptychocysts are the most taxonomically restricted in distribution, occurring only in the anthozoan order Ceriantharia. Their function is to entangle bits of mud among their robust tubules to form the feltwork that constitutes the tube of these burrowing animals (Arai, 1997). Nematocysts occur in all classes of Cnidaria, but some of the 30-plus varieties of nematocysts are restricted to members of certain classes (Fautin and Mariscal 1991). The nematocyst is secreted from the Golgi apparatus of a cell termed a cnidoblast (Watson 1988). A cnida therefore is technically not an organelle, but one of the most complex secretory products known (Watson, 1988). The nematocyst, which can only fire once, is enclosed in a capsule inside the cnidoblast. The stinging structure varies according to species, but generally consists of a hollow coiled thread with barbs lining its surface (Figures 11).

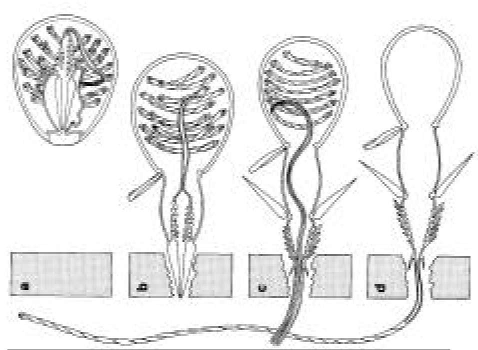


Figure 12. Steps of nematocyst discharge.

Nematocysts are concentrated on the tentacles or oral arms. A single tentacle can have hundreds or thousands of nematocysts embedded in the epidermis. Pressure within the nematocyst forces the stinging thread to rapidly uncoil and thousands of nematocysts acting as small harpoons fire into the prey injecting paralyzing toxins (Figure 12). Severity of stings depends on the species of jellyfish, the penetrating power of the nematocyst, the thickness of exposed skin of the victim and the sensitivity of the victim to the venom (Arai, 1997). Presently there is no toxicity scale for the sting of the jellyfish.

Orders

In the family Scyphozoa, there are four orders, 24 families, 71 genera and over 220 species. Jellyfish are divided into four orders based on morphological differences and distribution. The four orders of Scyphozoa are Coronatae, Semaeostomae, Rhizostomae and Stauromedusae. To better gain an appreciation of the diversity of these animals, descriptions of the orders and families follows, in some cases, an individual species will be discussed. (All morphological descriptions are taken from Meyer (1910) and Kramp (1961) unless listed otherwise.)

Order Coronatae

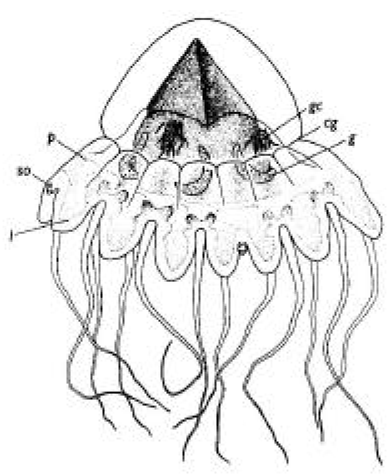


Figure 13. *Periphylla periphylla*. Cg-coronal groove; g-gonad; gc-gastric cirri; l-marginal lappet; p-pedalion; so-marginal sense organ.

This order is divided into 6 families, 12 genera and approximately 46 species. The order Coronatae includes bathypelagic (deep sea) to mesopelagic (medium sea depth) medusae. Each bell has a deep furrow, or a coronal groove that divides the aboral surface into a central disc and a peripheral area (Figure 13). The Coronatae have a single mouth with simple lips which are on a short manubrium. This order is generally considered to be the most primitive of the scyphozoa, many of which are very large and deep red to purple in color.

The life cycle of the Coronatae medusae is largely unknown. The polyps are solitary or colonial with periderm tubes made from chitin.. The juvenile medusae are made by transverse fission (strobilation) and go on to develop into sexual adult medusae. Some species lack the medusae phase and reproduce sexually within the periderm tubes.

Atollidae: This family contains one genus *Atolla* and three species (Appendix A). The family is distinguished by possessing more than eight marginal sense organs which alternate with an equal number of tentacles. The marginal lappets are twice as numerous as the tentacles. They are rare on the surface on the water and range in size from 12 to 150 mm wide depending on the species. *Atolla parva* is a deep sea medusae always with one long trailing tentacle, the function which is still unknown. (Whether or not it is in the same location on every animal is also unknown.) The medusae from this family are deep-sea animals that inhabitant oceans worldwide. Large numbers of *Atolla* have been taken from open dragnets between 350 and 2500 fathoms. They have been recorded in the North Atlantic, Indian Ocean, off the Cape of Good Hope, Africa, Antarctic, Tropical Pacific, Atlantic and Pacific Oceans. (This extremely wide distribution is mentioned because many of the family descriptions that follow have similar distributions and only exceptional distribution locations will be mentioned hereafter.)

Atorellidae: This family contains one genus *Atorella*, with four species (Appendix A). Atorellidae are distinguished by having exactly six rhopalia, six tentacles, 12 marginal lappets and 12 pedalia, and are from 5 to 17 mm wide at the bell. The family is marked by having four lips and four internal orange-colored gonads, while the rest of the body is colorless. It is not known how the number six was derived in this family. One hypothesis is that it was derived from *Atolla*. They have been recorded off the pacific coast of Panama and east coast of Africa.

Linuchidae: This family contains two genera *Linantha* and *Linuche*, with three species between them (Appendix A). They are set apart by having eight rhopalia and eight radial tentacles and eight gonads grouped in four pairs, the body being about 13 mm wide and 16 mm high. *Linuche unguiculata* is known to inhabit the tropical Atlantic and differs from *L. draco* by not having a marginal ring canal and three rows of subumbrella wart instead of two as found in *L. draco*. *L. draco* inhabits the Cina Sea. This rest of this family is widely distributed over the tropical Pacific and Indian Oceans. The other genus in this family *Linantha* is marked by having four interradial horseshoe shaped gonads, no subumbrella and is found near the Galapagos Islands.

Nausithoidae: This family contains three genera *Nausithoe, Stephanoscyphus* and *Palephyra*, with 26 species between them (Appendix A). Members of this family, 9 to 35 mm wide, are characterized by eight marginal sense organs and eight tentacles, and eight non-pair grouped gonads. The scyphostoma larva of *Nausithoe* infest sponges and appear similar to a branched hydroid. The medusa of *Nausithoe* has small clusters of crystalline cysts scattered at intervals within the ectoderm of the umbrella. *Stephanoscyphus* (Figure 14) is a solitary scyphopolyp endemic to submarine caves in the Western Mediterranean. The medusa stage is represented only in the embryonic stage. The specialized lifestyle of these animals can be viewed as an adaptation to the unique conditions found in the submarine caves. *Palephyra* is known to inhabit the waters of the tropical Indian Ocean near Madagascar and off the coast of China. *Palephyra* is only 8 mm high with light red gonads.

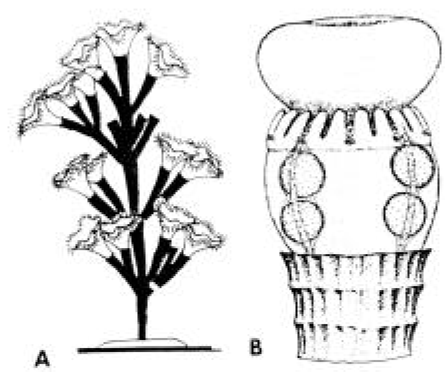


Figure 14. *Stephanoscyphus* as in its two forms. A) scyphopolyp. B) the embryonic medusa about to be released.

Paraphyllinidae: This family contains one genus, *Paraphyllina,* and three species (Appendix A). This family differs from Periphyllidae only by having marginal sense organs perradial instead of interradial. Found at 500 fathoms near Naples and the Malay Archipelago.

Periphyllidae: This family contains four genera, *Nauphantopsis*, *Pericolpa*, *Periphylla*, and *Periphyllopsis* with seven species between the genera (Appendix A). This family is characterized by having four interradial pedalia bearing tentacles which have marginal sense-clubs with four or more tentacles. The species can be found in the Antarctic, east of Australia and near New Zealand from a depths of 180 to 900 meters. Some members possess oval shaped gonads. *Periphylla* is one of the most spectacular deep sea medusae, not only because of its beauty, its interesting shape, but also because of its shear size, growing up to 80 mm high and 42 mm wide. Periphyllidae have very wide distribution (Appendix).

Order Semaeostomeae

This order is divided into 3 families, 5 subfamilies, 19 genera and approximately 56 species. The adult Semaeostomeae possesses large saucer-shaped bells having scalloped margins. The gastrovascular cavity has radial channels or canals that extend from the central stomach to the bell margin. This order has marginal sense organs with sensory clubs (rhopalia) which are formed from some of the niches between the lappets and four oral arms surrounding the central mouth. Most species posses a number of hollow tentacles on the umbrella margin. A system of canals or radial pouches can be found around the stomach. The planula may develop directly into medusae or into solitary non-tubed scyphistomae forming ephyrae. The medusa of this family are distinguished from the Coronatae by the development of the four perradial corners of the mouth which extend outward. Four long mouth-arms carry the free edge of the lips which have double curtain-like fringes. This order contains the slowest swimming medusae in the world, *Deepstaria,* which can be observed at depths around 600 meters. Semaeostomeae are common throughout all the oceans of the world.

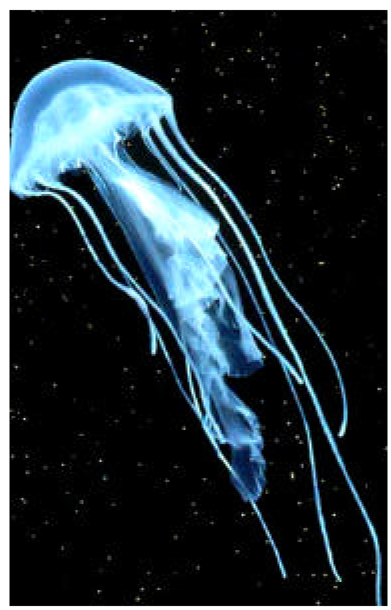


Figure 15. *Chrysaora quinquecirrha.*

Pelagiidae: In this family are three genera, *Chrysaora*, *Pelagia*, and *Sanderia* with 15 species between the genera (Appendix A). The characteristics of the family include 8 or 16 marginal sense organs and 8 or more tentacles. The bells are 100 to 400 mm wide, and 40 to 100 mm high. Medusa from the genus *Pelagia* develop directly from the planula, bypassing the sessile scyphostoma stage. This family is distributed world wide but is more abundant in warm waters such as the Mediterranean, African waters and the coast of Brazil where they are known to group in swarms in bays and estuaries. This family is closely related to Cyanidae except the tentacles arise singly in Pelagiidae and in clusters in Cyanidae. The most known Pelagiidae is the Sea Nettle (*Chrysaora quinquecirrha*, Figure 15). The sea nettle is frequently observed in the eastern United States and North Atlantic during summer months. This jellyfish is saucer-shaped with brown or red pigments, usually 180 mm in diameter. Four oral arms and long marginal tentacles hang from the bell. The stings are considered moderate to severely painful. The symptoms from sea nettle stings are similar to those of the Lion's Mane (*Cyanea capillata*).

Cyaneidae: This family contains three genera, *Cyanea*, *Desmonema*, and *Drymonema* with 17 species between the genera, 13 from *Cyanea*. The characteristics of the family include development through the sessile scyphostoma which strobilates and gives off ephryrae which develop into medusae. Members of this family are universal in distribution and are found in great numbers in warmer waters as well as colder waters. Unlike Pelagiidae, Cyaneidae are found in shallower water, not out in the open sea. Cyaneidae have a single, four sided mouth surrounded by four curtain like lips. Tentacles are usually formed in clusters. The most famous member of Cyaneidae is the Lion's Mane jellyfish (*Cyanea capillata*, Figure 16). This jelly is also known as the winter jelly. The Lion's Mane typically appears during colder months of the year. The bell, measuring around 200 mm, is saucer-shaped with reddish brown oral arms and eight clusters of tentacles hanging underneath. *Cyanea* are generally considered moderately painful to humans. Symptoms are similar to those of the moon jelly (*Aurelia aurita)*, but usually the pain is relatively mild and often described as burning rather than stinging. (This jellyfish was made famous by Sir Arthur Conan Doyle's mystery "The Adventure of the Lion's Mane.")

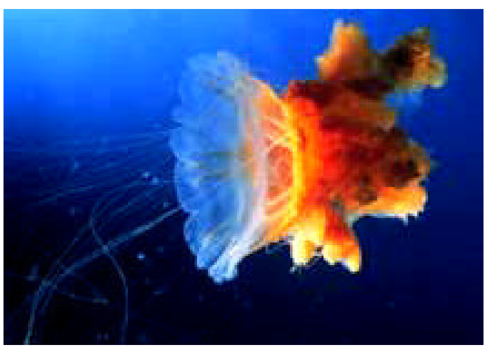


Figure 16. The Lion's Mane jellyfish, *Cyanea capillata***.**

Ulmaridae: This family contains five subfamilies, 13 genera, with 24 species between the genera (Appendix A). Ulmaridae have four internal gonads, four mouth arms with folded curtain-like margins and hollow tentacles. The medusae of this family are closely related to Cyaneidae but differ in that their radial canals are placed in intercommunication by means of a marginal circular canal.

Figure 17. The Moon Jelly *Aurelia aurita*.

Subfamily Aureliinae: There are two genera, *Aurelia* and *Aurosa*, with eight species in this subfamily (Appendix A). Aureliinae possesses numerous tentacles from the sides of the umbrella above the margin. The gonads are invaginated sacs and the medusae have four simple or separated mouth-arms. The genus *Aurelia* is among the most widely distributed of all Scyphozoans in the world — these jellyfish occur in all oceans and all latitudes. They are most abundant close to shore and rarely occur out in the open sea. Aureliinae are generally 50 to 250 mm wide at the bell. Most notable of this subfamily is the Moon Jelly (*Aurelia aurita*, Figure 17) which is the most studied probably the most widely recognized jellyfish in the world. It has a transparent, saucer-shaped bell and is easily identified by the four pink horseshoe-shaped gonads visible through the bell. It typically reaches 200 mm in diameter, but some are known to exceed 500 mm. The moon jelly is only slightly venomous to human contact and can produce symptoms from immediate prickly sensations to mild burning. The pain is usually restricted to the immediate area of contact.

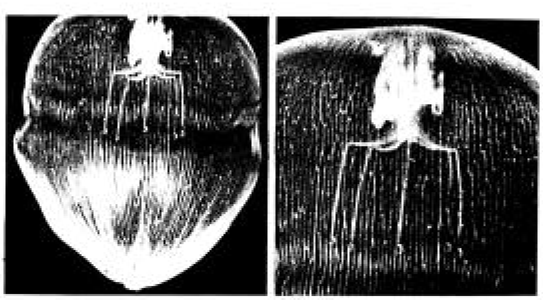


Figure 18. *Deepstaria enigmata*.

Subfamily Deepstaria: This subfamily is composed of one genus *Deepstaria* and two species (Appendix A). Deepstaria was named after the deep sea submersible Deepstar 4000 that first collected a specimen. Having been discovered in 1966 at a depth of 600 meters in the Catalina Basin off the coast of California, Deepstaria (Figure 18) is a relatively recent addition to the Scyphozoans (Larson, 1988). Another specimen was found at 950 meters off the coast of Bermuda the next year. This subfamily has the distinction of being the slowest swimming of the scyphozoans. Deepstaria have a large thin walled umbrella, no tentacles and capture their prey by closing the bell shut around the prey (Larson, et al 1988).

Subfamily Sthenoniinae: This subfamily has three genera *Phacellophora*, *Poralia* and *Sthenonia*, and three species in its members (Appendix A). Sthenoniinae are marked by having tentacles arise in linear clusters from the floor of the umbrella, 8 to 16 marginal sense organs and four bag-like gonads.

Subfamily Ulmarinae: This subfamily contains six genera, *Diplulmaris, Discomedusae*, *Floresca*, *Parumbrosa*, *Ulmaris* and *Undosa* and 11 species (Appendix A). The subfamily is characterized by There is speculation whether this subgroup is not just another subfamily at a young stages of medusa (Meyer 1910). The tentacles arise from between cleft in the lappets, not from the floor of the subumbrella. (In young *Cyanea*, the tentacles first appear in clefts between lappets and later the margins grow outward.) The bells are around 50 mm wide and 30 mm high with eight sense organs.

Subfamily Stygiomedusinae: This subfamily contains one genus, Stygiomedusinae, and two species. Stygiomedusinae are known for their symbiotic relationship with fish. The fish *Merlangius merlangus* seek shelter under and within the tentacles where they eat free-living animals like small crustacea (Tolley, 1987). The animals are approximately 500 mm wide at the bell, disk shaped and have large stomachs. There are 40 radial canals leaving the stomach, 20 rhopalia and the creatures are generally deep brown in color. These jellyfish reproduce asexually in a specialized brood chamber.

Order Rhizostomeae

This order is divided into 2 suborders, 11 families, 16 genera and approximately 89 species. The bell of the medusa lack tentacles and the oral arms of the manubrium are branched and bear deep folds into which food passes. The folds are secondary mouths and lead into arm canals which then pass into the stomach. The original mouth was lost due to fusion of the oral arms. This order contains medusae which lack pedalia, coronal grooves, a central mouth and marginal tentacles (Figure 1.8, 1.9, 8.5 in blue book). Four pairs of oral arms fuse from the manubrium and form a number of mouth openings. The marginal umbrella is divided into eight or more lappets. Each lappet possesses eight or

16 sense organs. A network of canals is found in the peripheral zone around the stomach. This order may reproduce by budding or strobbilate forming ephyrae as seen in Semaeostomeae. Rhizostomeae are found in the tropics and subtropics in shallow waters (Ruppert, 1994). Naming in this order is somewhat different depending on the source that is examined. This summary will be based on Meyer (1910).

Suborder: Kolpohorae

Included in this suborder are five families, ten genera, and 46 species. The hallmarks of this suborder are that the mouth-arms are three-winged or triangular. The network of canals enable communication with the central gastrovascular cavity in several places between the radial canals. The rhopolar pits are smooth and without radial folds.

Cassiopeidae: This family possesses one genus, *Cassiopea*, and 10 species (Appendix A). The family is marked by very branched mouth-arms which have numerous mouth openings and vesicles. There are four gonads and four separated subgenital cavities. This family possesses more than eight marginal sense organs. *Cassiopia* (Figure 19) possesses a symbiotic algae (zooanthella) in its mesoglea, and in sufficient light the jellyfish can survive solely on the products of the algal photosynthesis. Common in the waters of Florida and the West Indies, they rest upside down on the bottom of mangroves and trap small animals with their small delicate oral arms. The food is then carried to one of their many secondary mouths by canals in the arms. These arms then open to the stomach.

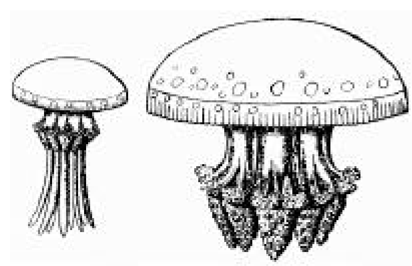


Figure 19. *Cassiopea andromeda* and *Cassiopea picta*.

Cepheidae: This family possesses four genera, *Cephea*, *Cotylorhiza*, *Netrostoma* and *Polyrhiza*, and 15 species (Appendix A). Members of this family have eight separate mouth-arms, the lower ends of which forms two expanding leaf-like side walls. The radial muscles are well developed and the ring muscles are weakly developed. Cepheidae can be found in abundance in the warmer tropical waters.

Mastigiidae: This family possesses three genera, *Mastigias, Mastigietta*, and *Phyllorhiza* and 14 species (Appendix A). Mastigiidae are recognized by the three winged mouth-arms that terminate in a club shaped extremity. The mouths are developed along the edges of the wings from the lower mouth arms and over their flat sides. Many species have 80 marginal lappets. The bells are sometimes flatter and range from 30 to 120 mm wide. Each of their 8 rhopalia have a pigmented mass of crystalline on them. Mastigiidae are closely related to *Pseudorhiza*, but have numerous complete radial canals. These species have only been found in warmer waters and have colors ranging from blue to yellow-orange to brown, some even have white spots ringed with black. Mastigiidae are known to be fast swimmers.

Thysanostomatidae: This family possesses one genus, *Thysanostoma*, and three species (Appendix A). These animals have large narrow lash-like frilled mouth arms. The upper parts of the mouth-arms are very short and partially fused to the arm disk by a series of arches reaching from one to the next. The bells can be from 90 to 120 mm wide and the eight mouth arms are from one and a half to three times as long as the bell is wide. The lower arms are three winged and Y or T shaped in cross section through its length.

Versurigidae: This family possesses one genus, *Versurgia*, and four species (Appendix A). This family has a flat bell that is shaped like a shield and ranges from approximately 60 mm wide, to 200 mm wide. Eight rhopalia are set within very shallow niches in the bell margin. This is a poorly described family; many of the species are described from a single specimen.

Suborder: Daktyliophorae

Included in this suborder are five families, 15 genera and 43 species (Appendix A). In this suborder the mouth-arms are three winged and the rhopolar pits have radial folds.

Lychnorhizidae: This family possesses three genera, *Anomalorhiza, Lychnorhiza*, and *Pseudorhiza*, and six species (Appendix A). This family is set apart by having three leafed or winged mouth-arms with no club-shaped appendages between the mouths. The stomach gives rise to 8 to 16 radial canals and a simple gastrovascular network. Another common feature is the lack of a common central mouth.

The bell is often from 120 to 600 mm wide and flatter on top than a hemisphere. This familiy can be found near the Philippines.

Catostylidae: This family possesses six genera, *Acromitoides, Acromitus, Catostylus, Crambione, Crambionella* and *Leptobrachia*, and 22 species (Appendix A). The mouth-arms of this family have no clubs, filaments or other appendages. This family is very closely related to Lychnorhizidae, the difference being that Catostylidae has neither filaments nor clubs on the mouth-arms. This family appears to prefer brackish, muddy harbors and may have many commensal plant cells within them giving Catostylidae a yellow-brown color. In specimens that do no have the plant cells within them, their color is cobalt blue. This family is abundant in the Indo-Pacific region and 3 species are found near the Atlantic coast of Africa and Europe. In the species *C. tagi*, the bell can get up to 500 mm wide.

Lobonnematidae: This family possesses two genera, *Lobonema*, and *Lobonemoides*, and five species (Appendix A). The mouth arms in this family are known to have greatly extended marginal lappets that taper to end points and have numerous filaments. The mouth arm membranes are perforated with window-like openings. This family also has 8 rhopalia and 196 ring canals. There are also numerous tapering nematocyst bearing papillae above each rhopalium. They also have a flatter bell and measure around 250 mm across. The stings have been known to be fatal to humans.

Rhizstomatidae: This family possesses three genera, *Eupilema*, *Rhizostoma*, and *Rhopilema*, and seven species (Appendix A). This family was derived by elongating the mouth-arms and reducing the expansion of the arms. The most common is the Mushroom Jelly (*Rhopilema verrilli*). The Mushroom Jelly is often mistaken for the Cannonball Jelly, but it differs in many ways. The Mushroom Jelly can grow up to 20 inches in diameter, lacks the brown bands associated with the cannonball and is much flatter and softer. Like the cannonball, the mushroom has no tentacles, however, it possesses long finger-like appendages hanging from the feeding apparatus. The Mushroom Jelly does not represent a hazard to humans.

Stomolophidae: This family possesses one genus, *Stomolophus*, and three species (Appendix A). This family has a central mouth opening with well developed, tube like manubrium that have been formed by

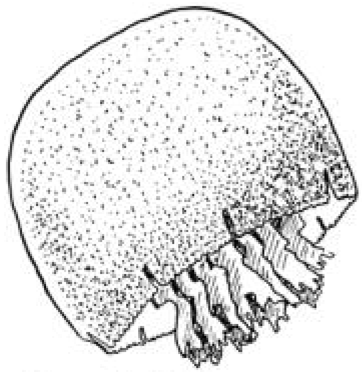


Figure 20. The Cannonball Jelly (*Stomolophus meleagris*).

the fusion of the lateral edged of what was 8 primitive mouth-arms. Only the ends of the mouth-arms are free and they are very branched. There are also four separate inverted gonads. These jellyfish rarely grow larger than 200 mm in diameter. *Stomolophus* are common along the eastern Americas. The most common is the Cannonball Jelly (*Stomolophus meleagris,* Figure 20), also know as jellyballs, these jellyfish are very common along the east coast of the United States. During the summer and fall, large numbers of *Stomolophus* appear near the coast and the estuaries. They are considered to be pests by commercial trawl fishermen because they clog and damage nets and slow sorting and trawl times. Fortunately for swimmers, while the Cannonball Jelly is the most abundant jellyfish in the area, it is also one of the least venomous. The half-spherical white bell with chocolate-brown bands can identify the Cannonball Jelly. They have no tentacles but a gristle-like feeding apparatus formed by the joining of the oral arms.

<u>Order Stauromedusae</u>

This order is divided into 3 families, 6 subfamilies, 15 genera and approximately 36 species. Stauromedusae are sessile scyphozoans attached by a stalk on the aboral side of the trumpet-shaped body. Mostly found in cold coastal waters. These jellyfish are considered the most unusual of the scyphozoans. They are jellyfish, but they attach themselves to seaweed and other objects by an aboral stalk. They are sometimes viewed as a permanently juvenile animal that never quite completes the transformation into the medusae form common in the other orders of scyphozoa. They keep many primitive characteristics that may give some clue as to what the scyphozoans looked like when they diverged from the hydrazoan line. The two most common stauromedusaens are *Lucernaria* and *Haliclystus,* being found mostly in cool water than in warmer water. They are usually 30 to 50 mm across, have a centrally located mouth at the end of a short manubruim. The oral surface is formed from

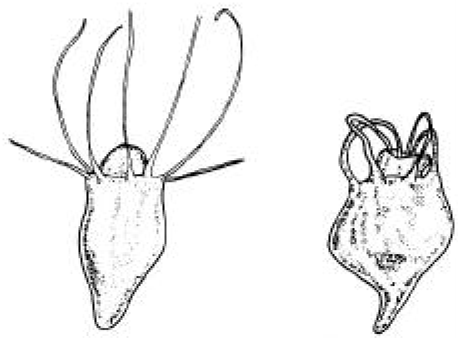


Figure 21. Polyp before and during feeding. The polyp inserts the tentacles into the mouth and "licks" the food from the tentacles.

lobes on which the tentacles are located. Unlike other scyphozoans, the medusae in this order are always sessile and develop directly from the scyphistoma stage without strobilation. One juvenile can arise from each scyphistoma. Each planula larvae can bud off other genetically identical planulae so that many genetically identical juveniles can come from a fertilized egg. The planulae are non-cilitated, and can creep unlike other cnidarians. The adult attaches itself to firm substrates by using its central adhesive disc. Some species can move from location to location by creeping, some are attached permanently, but none of the species are able to swim (Arai, 1997). Stauromedusae have a funnel shaped body and each of the eight arms (sometimes four bifurcated arms) terminates in a cluster of hollow, terminally knobbed tentacles. There are no sense organs in the mature medusae. Reproduction is year-round in most species and is accomplished by secreting gametes directly into the water where the planula develop. There is no sexual reproduction and the life span can last for several years.

Cleistocarpidae: This family contains three subfamilies, seven genera and 11 species (Appendix A). Cleistocarpidae are distinguished by having four perradial stomach pouches, each divided into and inner and an outer space by a transverse circumferential membrane or claustrum. The claustrum connects the gonads which are imbedded in the endoderm of the inner space. *Craterolophus*, a Cleistocarpidae with eight radial lobes and eight radial clusters of terminally knobbed tentacles, does not have perradial or interradial anchors or papillae.

Subfamily Depastrinae: This subfamily contains two genera *Depastromorpha* and *Depastrum*, and a total of two species (Appendix A). This subfamily has 16 clusters of tentacles arranged in rows around the bell margin. The tentacles are hollow and terminate with a nematocyst-knob. Members of this subfamily have divided stomach pouches with a four sided throat tube and are found along the Northern coast of Europe.

Subfamily Thaumatoscyphinae: This subfamily is represented by three genera, *Brocheilla*, *Halimocyathus* and *Thaumatoscyphus* with four species (Appendix A). These scyphozoans have 8 adradial clusters of terminally knobbed tentacles, four interradial horseshoe shaped gonads and 8 adradial arms.

Subfamily Craterolophinae: This subfamily is represented by two genera, *Craterolophus* and *Manania* with five species (Appendix A). Craterolophinae have no perradial tentacles, 8 adraddial gonads, a four chambered stalk with eight marginal lobes on the bell. These animals may sometimes have eight small tentacles which creates some debate as to whether they are not actually a member of the genus *Halimocyathus*.

Eleutherocarpidae

This family is known to possesses 4 simple perradial stomache pouches. The family contains three subfamilies, 8 genera, and 25 species (Appendix A). It is sometimes refereed to as Haliclystidae. Occasionally this family is subdivided into the subfamilies Haliclystidae, Kishinouyeidae and Lipkeidae. *Haliclystus* is an example of the family is found around the British coasts with eight perradial and interradial marginal anchors. This species, has a peduncle with four perradial chambers, a calyx with eight well developed marginal lobes (arms) all about equidistant from each other and a coronal muscle that is divided into eight separate sectors.

Subfamily Lucernariinae: This subfamily has three genera, *Haliclystus*, *Lucernaria* and *Stenoscyphus*, with 15 species (Appendix A). This subfamily is found in the waters around Japan. These animals have a four chambered peduncle and eight clusters of tentacles. The stalk that attaches it to a substrate is four chambered and the stomach is four chambered.

Subfamily Kishinouyeinae: This subfamily contains three genera *Kishinouyea*, *Lucernariopsis* and *Sasakiella*, each having two species between them (Appendix A). These animals are very similar to the Lucernariinae, the difference being that when the young medusae develop, the four intradial septa unite and the peduncle changes to form four separate chambers. Their colors generally match their surroundings.

Subfamily Lipkeinae: This subfamily contains one genus, *Lipkea* and three species (Appendix A). This is the only Stauromedusae to have perradial and interadial marginal lobes. The bell is 7 to 8 mm wide and 4 mm high and has oval shaped mucous glands. The subumbrella is concave and the central mouth is elevated and surrounded by 4 lips. Very few have been observed.

Kyopiidae

This family has one genus, *Kyopoda*, and one species *K. lamberti*. This is the newest member of the Stauromedusae and was recently discovered in the waters off of Japan. In the order Stauromedusae, the stomach and gonads are normally found in the calyx. However, in Kyopiidae, they are found in a sac-like swelling at the base of the stalk (Larson, 1988). The systematic position within the order is unknown.

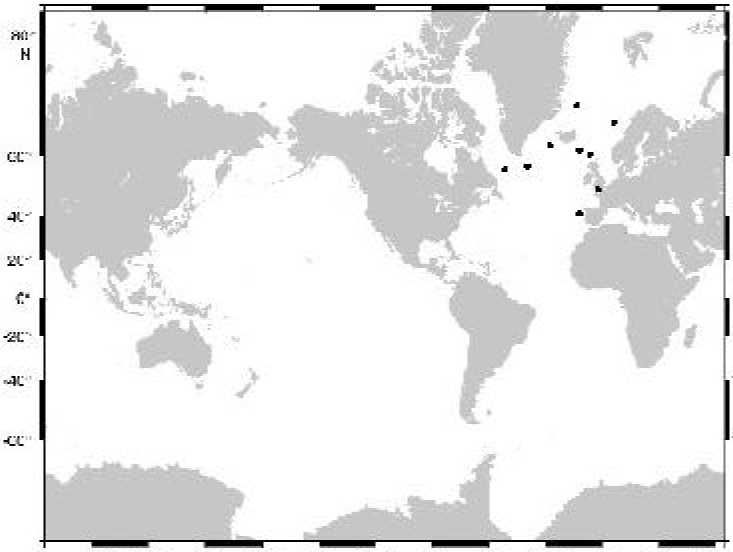
Summary

The diversity of scyphozoans is difficult to assess because they are ocean dwelling organisms. There may be many bathypelagic species that will yet be discovered. There are many reasons for the successful evolution of the class scyphozoa. Jellyfish have evolved to produce a very unique and efficient means of capturing various types of prey. Scyphozoans also have a short life span and an amazing lifecycle that can produce many offspring that are able to drift with the currants to be dispersed almost anywhere. Jellyfish are known to inhabit all levels of ocean, in all latitudes worldwide, which speaks of their adaptive abilities. For these reasons scyphozoans can be considered very successful at adapting to all oceanic habitats.

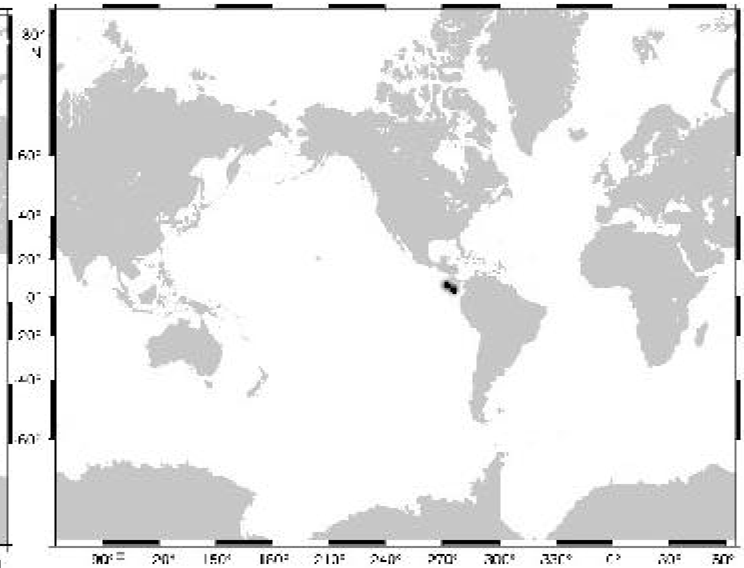
Jellyfish may appear to have no apparent value, but they are, in fact, a very important part of the marine food web. One species, the Mushroom Jelly, is even considered a delicacy by humans. Both fresh and pickled mushroom jellyfish are consumed in large quantities in China and Japan. Jellyfish are carnivorous, feeding mostly on a variety of zooplankton, comb jellies and occasionally other jellyfish. Larger species, however, are capable of capturing and devouring large crustaceans and other marine organisms. Jellyfish themselves are preyed upon by spadefish, sunfish, loggerhead turtles and other marine organisms. For these reasons, jellyfish can be considered an important part of the ecological food web as well as an important member of the pelagic world. As with the many other creatures of the sea that we know little about, the jellyfish warrants further research so that we may understand the extent of their diversity and the means in which they live.

Appendix A:

Maps and Figures



Distribution of family Atollidae



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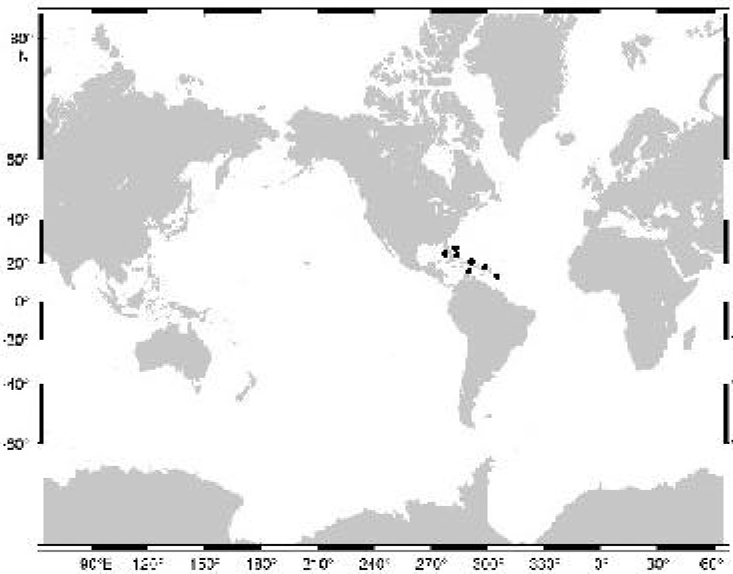
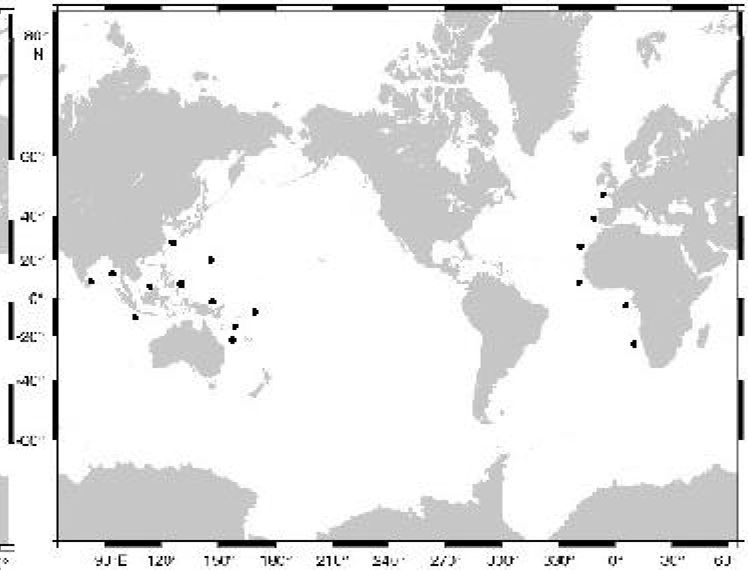


Distribution of family Cassopeidae



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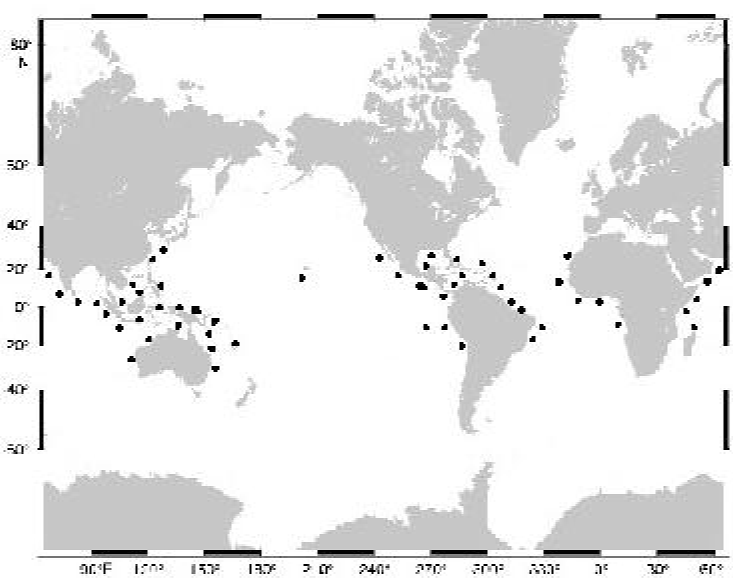
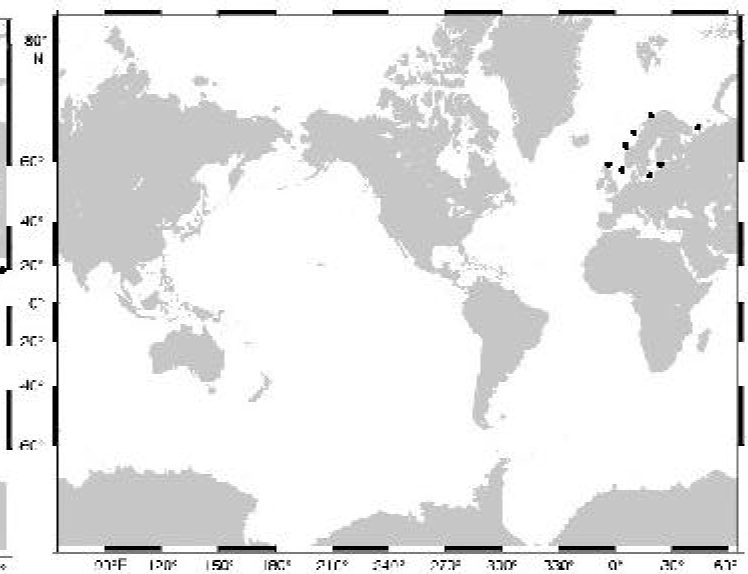
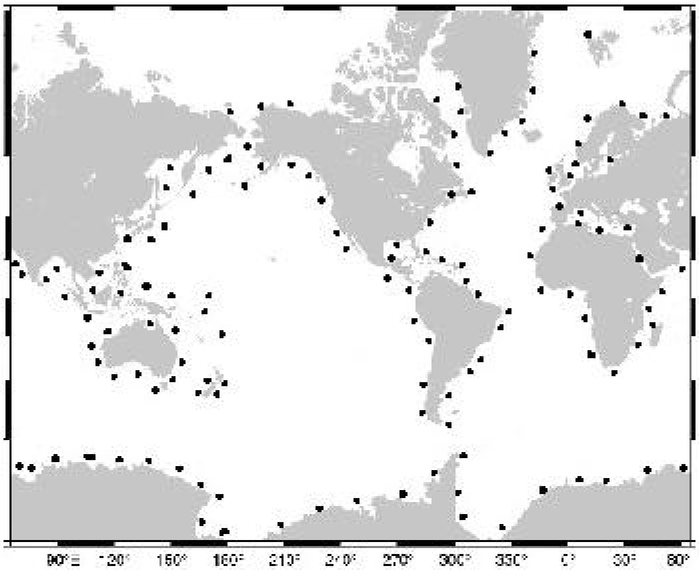


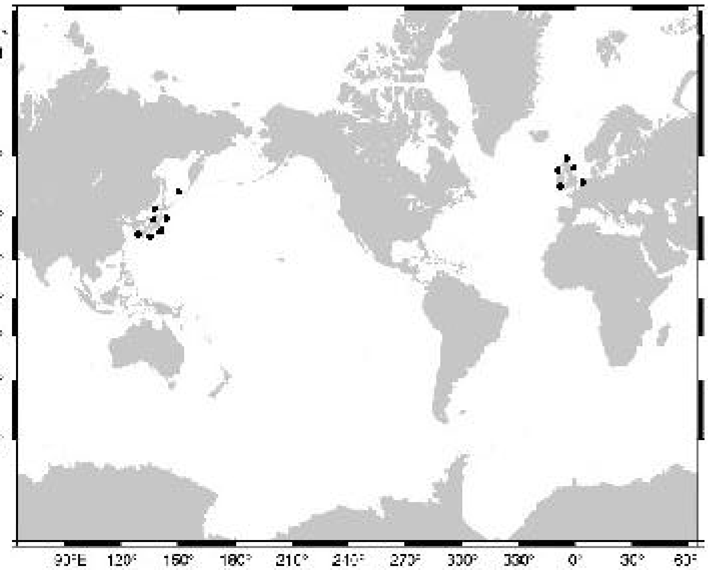
Distribution of family Cepheidae



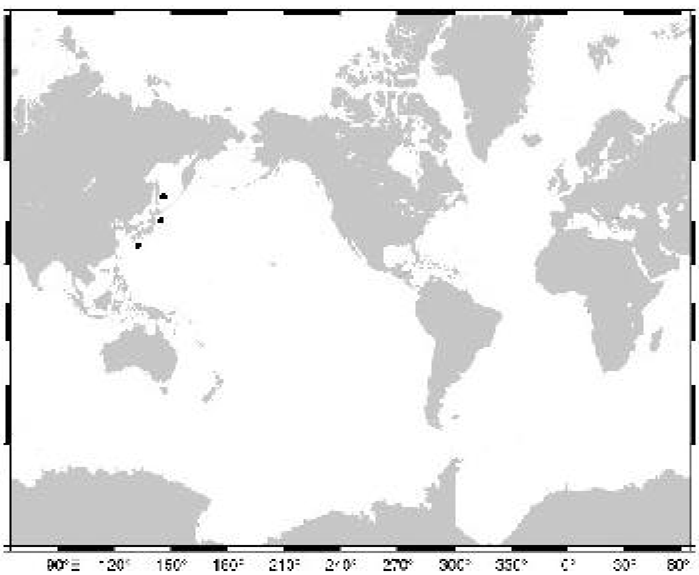
Distribution of family Cleistocarpidae



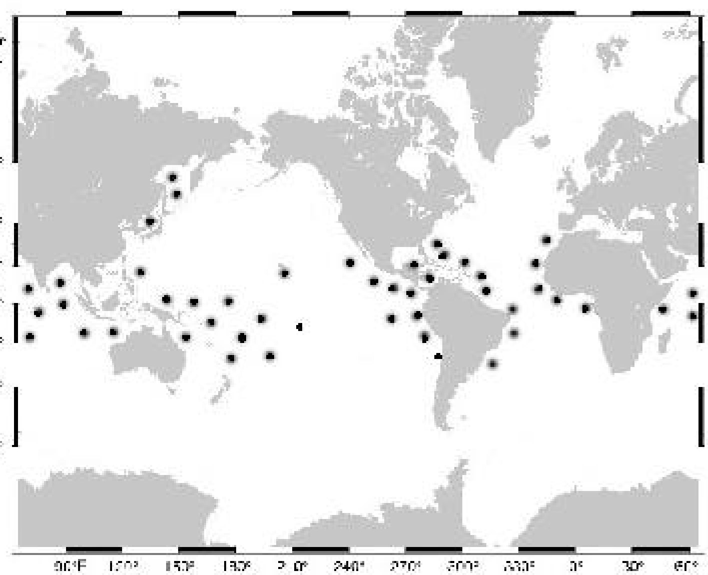
Distribution of family Cyaneidae



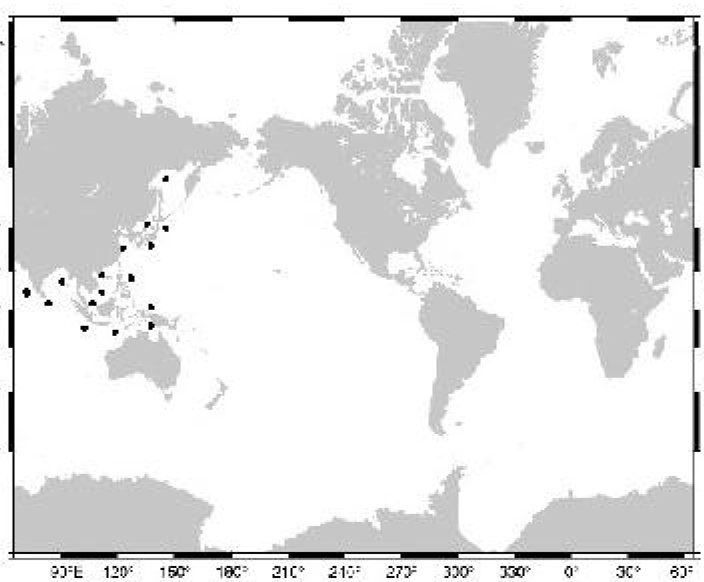
Distribution of family Eleutherocarpidae



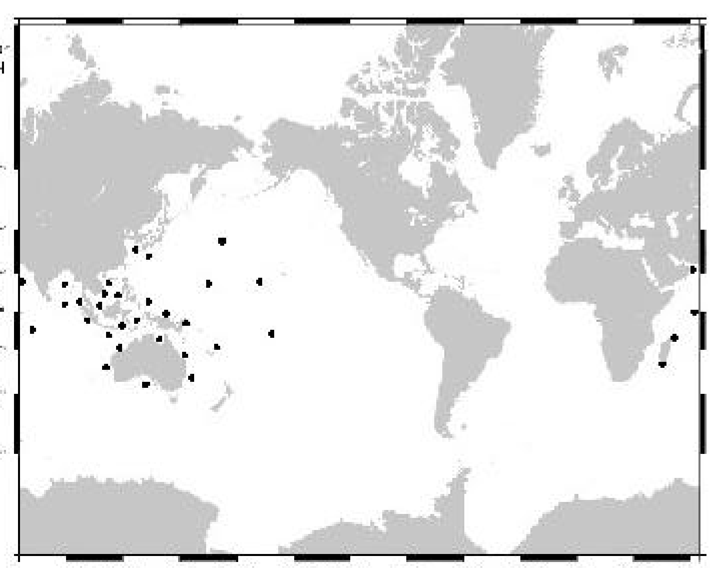
Distribution of family Kyopiidae



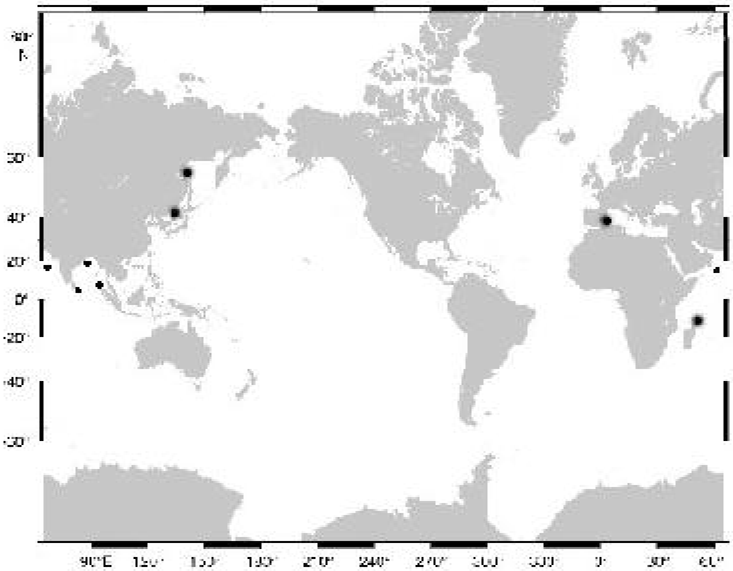
Distribution of family Linuchidae



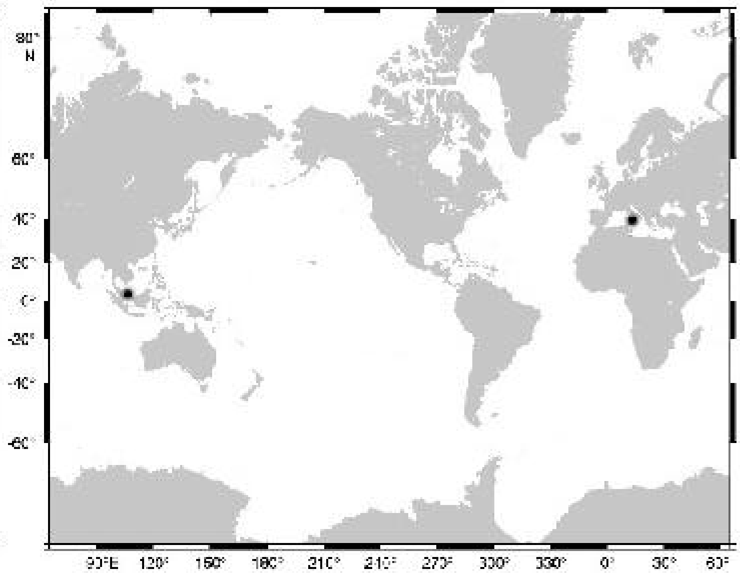
Distribution of family Lobonematidae



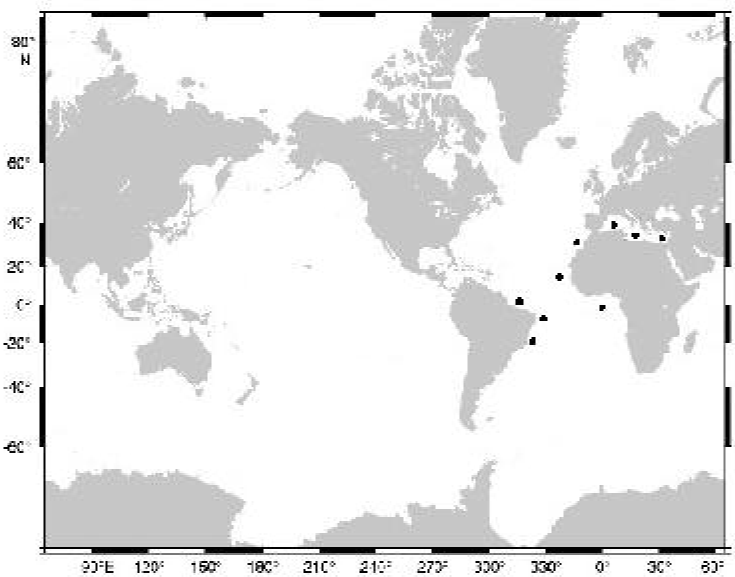
Distribution of family Mastigiidae



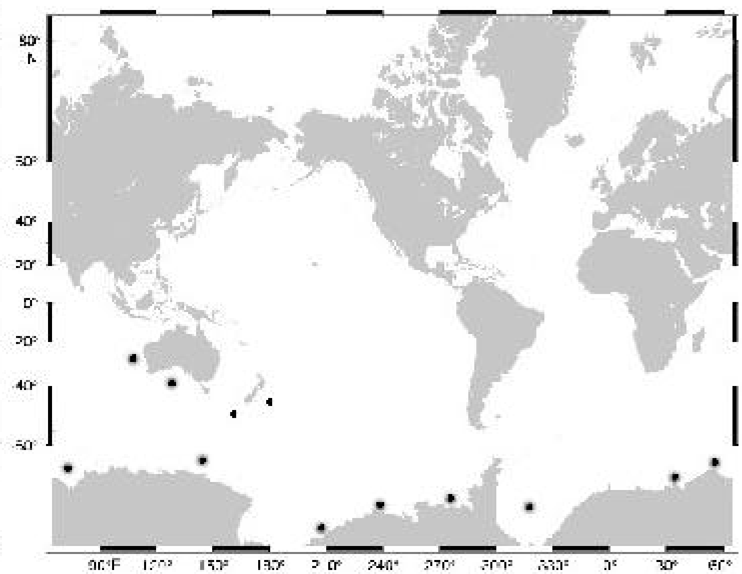
Distribution of family Nausithoidae



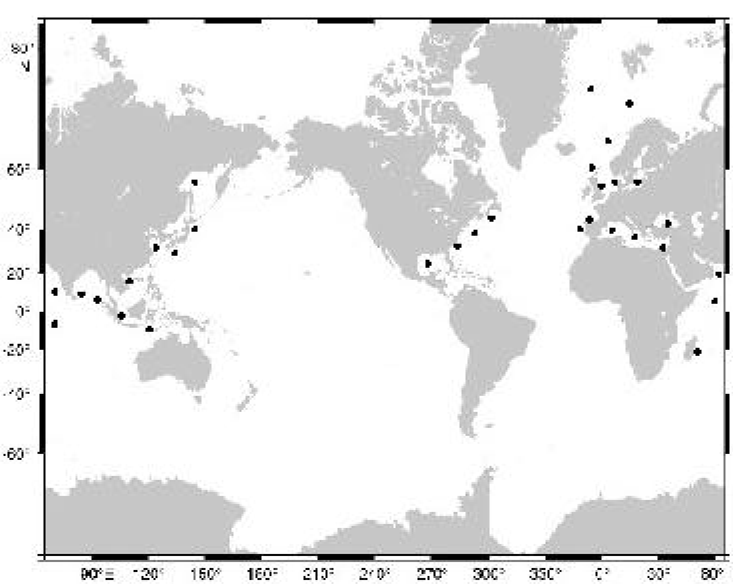
Distribution of family Paraphyllinidae



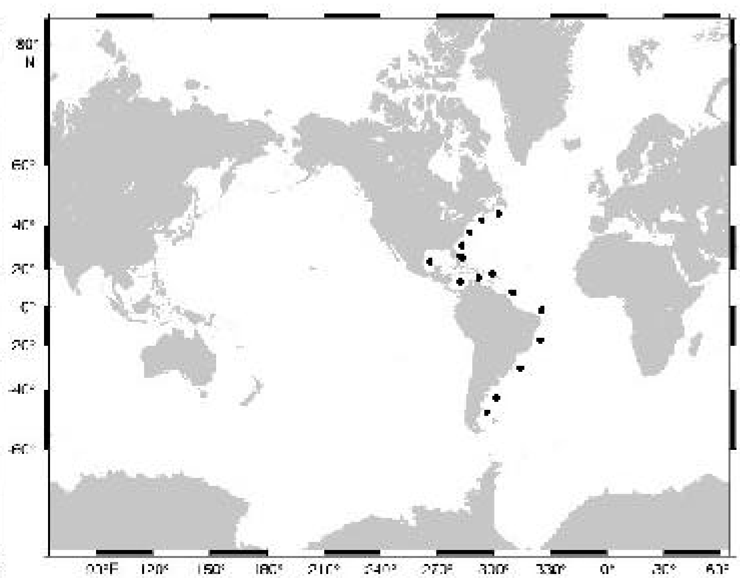
Distribution of family Pelagiidae



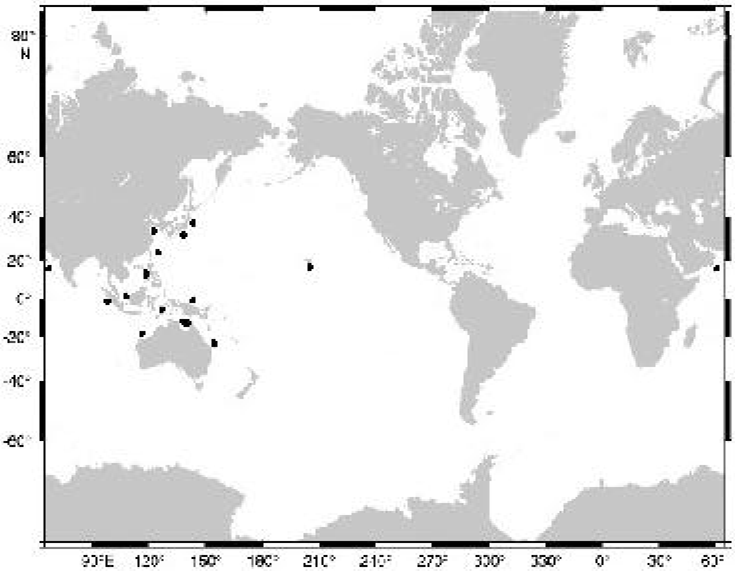
Distribution of family Periphyllidae



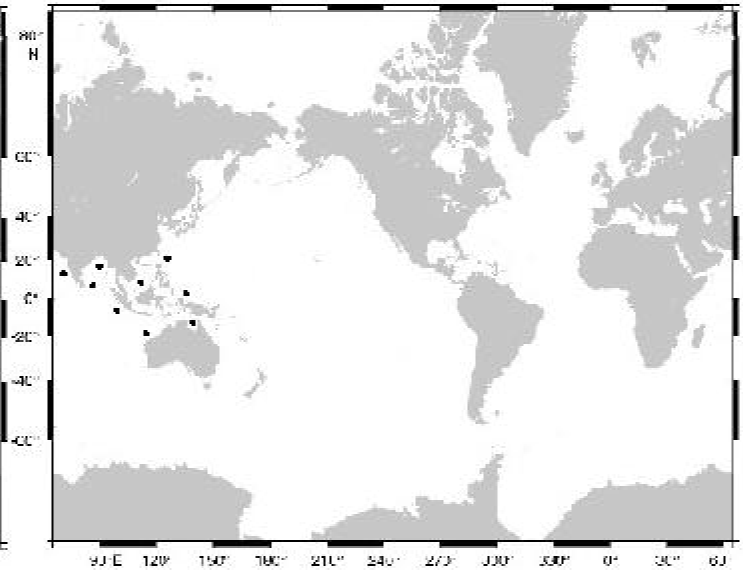
Distribution of family Rhizstomatidae



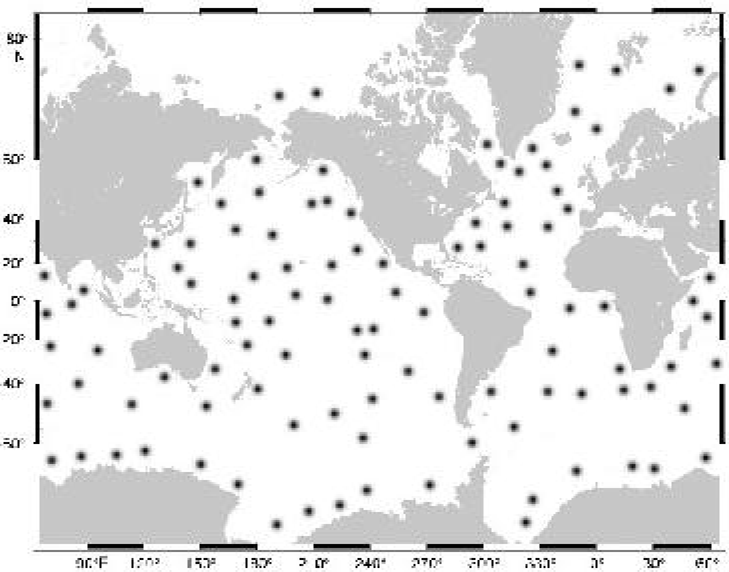
Distribution of family Stomolophidae



Distribution of family Thysanostomatidae



Distribution of family Versurigidae

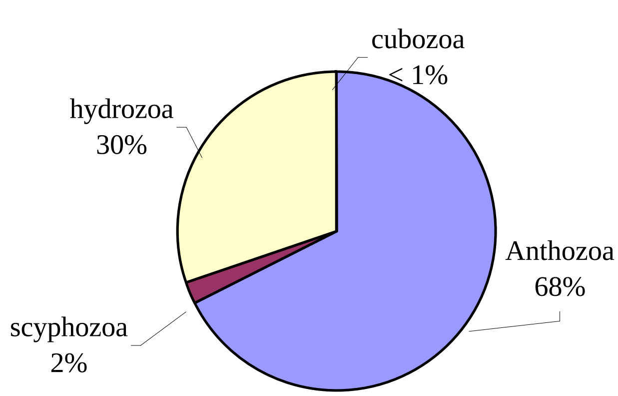


Distribution of family Ulmaridae

Similarities and differences between the classes of scyphozoa

	Stauromedusae	Coronatae	Semaeostomae	Rhizostomae
Development				
cleavage	total, equal	total, slightly unequal	total, slightly unequal	total, slightly unequal
gastrulation	unipolar immigration	unipolar immigration	invagination	invagination
planula	unciliated	ciliated	ciliated	ciliated
polyp	four tentacles, four septa, four gasyric pockets	four tentacles, four septa, four gasyric pockets	four tentacles, four septa, four gasyric pockets	four tentacles, four septa, four gasyric pockets
intermediate stage	none	ephyra	ephyra	ephyra
sexual phase	poly	medusa	medusa	medusa
Umbrella				
coronal grove	none	present	none	none
pedalia	none	present	none	none
marginal lappets	none	present	present	present
Marginal organs				
tentecles	present	present	present	none
rhopalar organs	rhopalioids	rhopalia	rhopalia	rhopalia
Subumbrellar organs				
manubrium	four oral arms	four oral arms	four oral arms	eight arms fused
subumbrella pits	peristomial pits	peristomial pits	subgenital pits	subgenital pits
Inner organs				
centrogaster	present	present	present	present
gastric pouches	present	present	none	none
septa	present	present	none	none
calustra	present	none	none	none
radia canals	none	present	present	present
ring canals	none	none	partly present	partly present
lappet pouches	none	present	present	present
gastric filaments	on septa	present	on subumbrellar entoderm	on subumbrellar entoderm
gonads	mesogon pouches exogon	in subumbrellar entoderm	in subumbrellar entoderm	in subumbrellar entoderm
musculature	more poylpiod	medusiod	medusiod	medusiod
nervous system	more poylpiod	medusiod	medusiod	medusiod

Taxonomic detail of Phylum Cnidaria
Percentage of species



Appendix B:

Classification of Scyphozoa
Families, genera and species

Sources for classifications were compiled from Kramp (1961) and Mayer (1910).

Appendix B

Order: Coronatae

Family	Genus	Species
Atollidae	*Atolla*	*A. parva*
		A. vanhoeffeni
		A. wyvillei
Atorellidae	*Atorella*	*A. arcturi*
		A. subglobosa
		A. vanhoeffini
		A. japonica
Linuchidae	*Linantha*	*L. lunulata*
	Linuche	*L. draco*
		L. unguiculata
Nausithoidae	*Nausithoe*	*N. antiqua*
		N. alatrossi
		N. atlantica
		N. challengeri
		N. clausi
		N. eumedusoides
		N. indica
		N. globifera
		N. limpida
		N. maculata
		N. marginata
		N. picta
		N. planulophora
		N. punctata
		N. racemosa
		N. rubra
		N. thieli
		N. werneri
	Stephanoscyphus	*S. corniformis*
		S. eumedusoides
		S. planulophorus
		S. racemosus
		S. simplex
	Palephyra	*P. antiqua*
		P. indica
		P. pelagica
Paraphyllinidae	*Paraphyllina*	*P. intermedia*
		P. ransoni
		P. rubra
Periphyllidae	*Nauphantopsis*	*N. diomedeae*
	Pericolpa	*P. campana*
		P. quadrigata

Family	**Genus**	**Species**
(Periphyllidae cont.)		
		P. tetralina
	Periphylla	*P. periphylla*
	Periphyllopsis	*P. braueri*
		P. galatheae

Order: Semaeostomeae

Pelagiidae	*Chrysaora*	*C. africana*
		C. blossevillei
		C. depressa
		C. fulgida
		C. fuscescens
		C. helvola
		C. hysoscella
		C. lactea
		C. melanaster
		C. pacifica
		C. plocamia
		C. quinquecirrha
	Pelagia	*P. noctiluca*
		P. colorata
	Sanderia	*S. malayensis*
Cyaneidae	*Cyanea*	*C. annasethe*
		C. buitendijki
		C. capillata
		C. citrea
		C. ferruginea
		C. fulva
		C. lamarcki
		C. mjobergi
		C. muellerianthe
		C. nozakii
		C. postelsi
		C. purpurea
		C. rosea
	Desmonema	*D. chierchianum*
		D. gaudichaudi
	Drymonema	*D. dalmatinum*
		D. gorgo
Ulmaridae		
Subfamily: Aureliinae	*Aurelia*	*A. aurita*
		A. coerulea
		A. colpota
		A. labiata
		A. limbata
		A. maldivensis

Family	Genus	Species
(*Aurelia* cont.)		
		A. solida
	Aurosa	*A. furcata*
Subfamily: Deepstariinae	*Deepstaria*	*D. enigmatica* *D. reticulum*
Subfamily: Sthenoniinae	*Phacellophora*	*P. camtscatica*
	Poralia	*P. rufescens*
	Sthenonia	*S. albida*
Subfamily: Ulmarinae	*Diplulmaris*	*D. antarctia* *D. malayensis*
	Discomedusae	*D. lobata* *D. philippina*
	Floresca	*F. parthenia*
	Parumbrosa	*P. polylobata*
	Ulmaris	*U. protoypus* *U. snelliusi*
	Undosa	*U. undulata*
Subfamily: Stygiomedusinae	*Stygiomedusae*	*S. fabulosa* *S. gigantea*

Order: Stauromedusea

Cleistocarpidae		
Subfamily: Depastrinae	*Depastromorpha*	*D. africana*
	Depastrum	*D. cyathiforme*
Subfamily: Thaumatoscyphinae	*Brochiella*	*B. hexaradiata*
	Halimocyathus	*H. lagena* *H. platypus*
	Thaumatoscyphus	*T. distinctus*
Subfamily: Craterolophinae	*Craterolophus*	*C. convolvulus* *C. macrocystis*
	Manania	*M. atlantica* *M. distincta* *M. gwilliami*
Eleutherocarpidae		
Subfamily: Lucernariinae	*Haliclystus*	*H. antarcticus* *H. auricula*

Family	Genus	Species
(*Haliclystus* cont.)		
		H. borealis
		H. salpinx
		H. steinegeri
		H. octoradiatus
	Lucernaria	*L. quadricornis*
		L. australis
		L. bathyphila
		L. haeckeli
		L. infundibulum
		L. quadricornis
		L. saint-hilarei
		L. walteri
	Stenoscyphus	*S. inabai*
Subfamily: Kishinouyeinae	*Kishinouyea*	*K. nagatensis*
		K. corbini
	Lucernariopsis	*L. campanulata*
		L. vanhoeffeni
	Sasakiella	*S. cruciformis*
		S. tsingtaoensis
Subfamily: Lipkeinae	*Lipkea*	*L. ruspoliana*
		L. stephensoni
		L. sturdzi
Kyopiidae	*Kyopoda*	*K. lamberti*

Order: Rhizostomeae

Suborder: Kolpohorae		
Cassiopeidae	*Cassiopea*	*C. andromeda*
		C. depressa
		C. frondosa
		C. medusae
		C. mertensi
		C. ndrosia
		C. ornata
		C. picta
		C. vanderhorsti
		C. xamachana
Cepheidae	*Cephea*	*C. cephea*
		C. conifera
		C. octostyla
		(3) undescribed species
	Cotylorhiza	*C. ambulacrata*
		C. erythraea
		C. pacifica
		C. tuberculata

Family	**Genus**	**Species**
(Cepheidae cont.)		
	Netrostoma	*N. coerulescens*
		N. dumokuroa
		N. setouchianum
		N. typhlodendrium
	Polyrhiza	*P. vesiculosa*
Mastigiidae	*Mastigias*	*M. albipunctatus*
		M. andersoni
		M. gracilis
		M. ocellatus
		M. pantherinus
		M. papua
		M. roseus
		M. sidereus
		(1) undescribed species
	Mastigietta	*M. palmipes*
	Phyllorhiza	*P. luzoni*
		P. pacifica
		P. peronlesueuri
		P. punctata
Versurigidae	*Versuriga*	*V. anadyomene*
		V. pinnata
		V. vesicata
		(1) undescribed species
Thysanostomatidae	*Thysanostoma*	*T. flagellatum*
		T. loriferum
		T. thysanura
Suborder Daktyliophorae		
Lychnorhizidae	*Anomalorhiza*	*A. shawi*
	Lychnorhiza	*L. arubae*
		L. lucerna
		L. malayensis
	Pseudorhiza	*P. aurosa*
		P. haeckeli
Catostylidae	*Acromitoides*	*A. purpurus*
		A. stiphropterus
	Acromitus	*A. flagellatus*
Catostylidae	*Acromitus*	*A. hardenbergi*
		A. maculosus
		A. rabanchatu
		A. tankahkeei

Family	**Genus**	**Species**
(*Catostylus* cont.)		
	Catostylus	*C. cruciatus*
		C. mosaicus
		C. ornatellus
		C. ouwensi
		C. perezi
		C. tagi
		C. townsendi
		C. tripterus
		C. viridescens
	Crambione	*C. bartschi*
		C. cooki
		C. mastigophora
	Crambionella	*C. orsini*
		C. stuhlmanni
	Leptobrachia	*L. leptopus*
Lobonematidae	*Lobonema*	*L. mayeri*
		L. smithi
	Lobonemoides	*L. gracilis*
		L. robustus
		L. sewlli
Rhizstomatidae	*Eupilema*	*E. scapulare*
	Rhizostoma	*R. luteum*
		R. pulmo
	Rhopilema	*R. hispidum*
		R. nomadica
		R. rhopalophorum
		R. verrilli
Stomolophidae	*Stomolophus*	*S. fritillarius*
		S. meleagris
		S. nomurai

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Figure 13: Cross section from Meyer 1910.

Figure 14: *Stephanoscyphus. F* from Barnes, 1980.

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Figure 18: *Deepstaria*. From Larson, 1988.

Figure 19: *Cassiopea andromeda* and *Cassiopea picta.* From Mayer 1910.

Figure 20: *Stomolophus meleagris*. From Mayer 1910

Figure 21:Polyp feeding. From Mayer 1910.

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