

Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria)

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The distribution of the 346 hydromedusan species hitherto recorded from the Mediterranean is considered, dividing the species into zoogeographical groups. The consequences for dispersal due to possession or lack of a medusa stage in the life cycle are discussed, and related to actual known distributions. There is contradictory evidence for an influence of life cycle patterns on species distribution. The Mediterranean hydromedusan fauna is composed of 19.5% endemic species. Their origin is debatable. The majority of the remaining Mediterranean species is present in the Atlantic, with various world distributions, and could have entered the Mediterranean from Gibraltar after the Messinian crisis. Only 8.0% of the fauna is classified as Indo-Pacific, the species being mainly restricted to the eastern basin, some of which have presumably migrated from the Red Sea via the Suez Canal, being then classifiable as Lessepsian migrants. The importance of historical and climatic factors in determining the composition of the Mediterranean fauna of hydromedusae is discussed.

ADDITIONAL KEY WORDS:—Hydrozoa – hydroid – medusa – dispersal.

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INTRODUCTION

The description and explanation of the distribution of organisms is the main goal of biogeography. The theoretical framework on which biogeographical analyses are usually based can be divided into two approaches: the historical and the ecological.

The historical approach implies that the distribution of a species reflects its evolutionary history, so that biogeographic and phylogenetic analyses are strictly related by taking speciation processes into account. The original version of the historical approach consists of the dispersal theory, typically accepted by Darwinian and Neo-Darwinian evolutionary biologists. According to this theory species originate mainly by allopatry due to dispersal of members of the ancestral population into separate geographic areas. The actual distribution of organisms is thus the result of the dispersal of their ancestors, being due to the intrinsic potential of the species, in terms of vagility.

In recent years the theories of historical biogeography have been changed by a different approach which has led to vicariance biogeography, with the integration of Croizat's panbiogeography (e.g. Croizat, 1964) and the cladistic method (e.g. Nelson & Platnick, 1981). Vicariance biogeography postulates that ancestral species were widely distributed before the fragmentation of the Pangaea and that continental drift led to physical separation of the original populations, leading then to speciation. The actual distribution of organisms, in this case, is due to extrinsic reasons, being caused by the fragmentation of the areas inhabited by their ancestors. A further development of this second approach led to cladistic biogeography (e.g. Humphries & Parenti, 1989), with the construction of cladograms for both phylogenies and areas of distribution.

A contradiction between these two theories is, however, apparent. They take into account two aspects of the history of life which are not mutually exclusive. The fragmentation of the Pangaea undoubtedly had a decisive impact on both speciation and distribution of organisms, but the possession of a wide distribution throughout the Pangaea (a starting point in vicariance biogeography) implied dispersal from a centre of origin or, less probably, instantaneous speciation on a worldwide scale.

The ecological approach (see, for instance, Davis, 1982; Endler, 1982; Blondel, 1986) states that historical factors are not necessarily linked to actual distributions, and that species are present in those localities where their ecological requirements are satisfied. Of course this condition must be valid for every theory, and also in this case there is not a real conflict with the historical approaches. Vermeij (1978) attempted to reconcile historical and ecological approaches in marine zoogeography.

These problems, however, have been tackled mainly in terrestrial organisms. Marine zoogeography, even in the light of the most modern approaches, is still

largely devoted to the determination of actual distributions. The unexplored portions of the world ocean are so vast that the descriptive stage is far from being completed (van der Spoel, 1983). Fishes and some invertebrates such as molluscs have better known distributions, but this is usually not the case for the rest of the faunas. Especially in invertebrates, marine biologists have mainly stressed the evolution of life-history traits and their relevance to dispersal (e.g. Valentine & Jablonski, 1983; Strathmann, 1985; Jackson, 1986), or have based the explanation of species distributions in terms of adaptations to local conditions (e.g. Vermeij, 1978, 1989). For some groups, such as molluscs, however, life-history traits have been used to explain distributions (e.g. Scheltema, 1986) and evolution (e.g. Jablonski, 1986).

Hydromedusae, in both their hydroid and medusa stages, occur commonly in all oceans and seas but a synthesis of their world distribution has never been attempted (see Kramp, 1959, 1961, 1968 for the medusa stage only). They have much-differentiated cycles (see below), and almost all reproductive and dispersal strategies of higher animals are already shown at the hydromedusan evolutionary level.

We have chosen to study the relationships of the hydromedusan fauna of the Mediterranean Sea because it is one of the better known in the world and because the geological history of the basin has been recently carefully reconstructed. The opening of the Suez Canal, connecting the Mediterranean and the Red Sea, furthermore, constitutes a rare opportunity for 'experimental' biogeography.

After a general description of the history and the physical conditions of the Mediterranean, and of the life-cycle types of hydromedusae, we will consider the affinities of the Mediterranean hydromedusan fauna, trying then to compare the actual distributions with the results expected by the application of the different biogeographic theories.

The Mediterranean Sea

The Mediterranean Sea is considered to be a relict of the Tethys Sea, the body of water separating Gondwana and Laurasia following the fragmentation of Pangaea. It connected the early Atlantic and Pacific Oceans. During the Miocene (Pontian) the eastern part of the Tethys Sea closed, and the only communication left was that with the Atlantic Ocean. When this connection closed as well, the Messinian crisis (between 6 and 5 Ma BP) led to the almost complete drying of the Mediterranean. Only the deeper parts of the basin seem to have retained water (see Maldonado, 1985 for a review of the geological history of the Mediterranean). Salinity, and probably temperature, were very high. The opening of the Strait of Gibraltar (5 Ma BP) restored the level of the sea. The Mediterranean relicts of the Tethys Sea, therefore, would have passed the Messinian crisis in almost non-marine conditions or in refuge areas. This possibly led to many local extinctions of both flora and fauna. The sea-grass *Posidonia* is the most outstanding case of Tethyan endemism: representatives of this genus live only in the Mediterranean and in Southern Australia. How the ancestral stock of the single Mediterranean species, *Posidonia oceanica*, survived the Messinian crisis is still debated and the same questions apply to the remainder of presumed Tethyan species (see Pérès, 1985, for a discussion).

Recent studies (see Por, 1989, for a review) are showing that the Messinian crisis was perhaps not so drastic throughout the basin as previously thought, so this topic is to be considered as not completely clarified.

Today the Mediterranean communicates with the Atlantic via the Strait of Gibraltar and with the Red Sea via the Suez Canal, opened in 1869.

The physico-chemical conditions of the Mediterranean are different from those of the Atlantic Ocean and the Red Sea. Deep-water temperature is constant at about 13°C. This is the mean temperature of the whole basin in the cooler part of the year (January–March), with slightly higher values in the eastern basin and very low values (4–5°C) in the northern Adriatic. Surface temperature can reach 28°C in August. In shallow waters, then, the temperature differences between the warm and the cold season can approach 15–20°C. Salinity is about 37‰, and so is higher than in the Atlantic (about 35‰) and lower than in the Red Sea (40–41‰). The eastern basin has salinities of up to 39‰. Strong seasonality is thus a striking feature of the Mediterranean. Temperature is the most variable factor, accompanied by variations in a number of other physical factors, including the concentration of nutrients, water movement and light penetration. A 'warm' season (May–June to October–November) thus alternates with a 'cold' season (November–December to April–May). Planktonic and benthic primary and secondary production show sharp seasonal cycles reflecting this alternation of climatic conditions.

Zoogeographical regions

Marine zoogeography is fairly advanced in some groups (especially vertebrates) but lower invertebrates such as Hydrozoa have received scant attention. The incompleteness of our knowledge even of the overall distribution of hydromedusae is exemplified by the situation in the Pacific insular area. The synopsis by Kramp (1968) is the standard work for the area and lists 59 species of Antho- and Leptomedusae. A long period of observation at a single site in Papua New Guinea raised the number to 176, with the description of 43 new species and 96 new records from the area (Bouillon, Clareboudt & Seghers, 1986). Some of these newly described species are now being found in the Mediterranean! It is hence inadvisable to divide the oceans into detailed regions and subregions.

The distribution patterns considered (Mediterranean Endemic, Mediterranean-Atlantic, Boreal, Tropical-Atlantic, Indo-Pacific, Circumtropical, Cosmopolitan) are, for convenience, taken to have the Mediterranean as their centre and are compared with it (Fig. 1). They apply then to the Mediterranean fauna and consider all the possible relations between this and other faunas. For instance, we consider as Indo-Pacific the species found both in the Mediterranean and the Indo-Pacific, even though an Indo-Pacific species should not necessarily occur in the Mediterranean.

Biological features of hydromedusae affecting their distribution

Hydromedusae are represented by a medusa, a planula and a polyp stage. The alternation of benthic and pelagic stages is a basic feature of hydromedusae, though in some orders the polyp is absent (some Narcomedusae and all

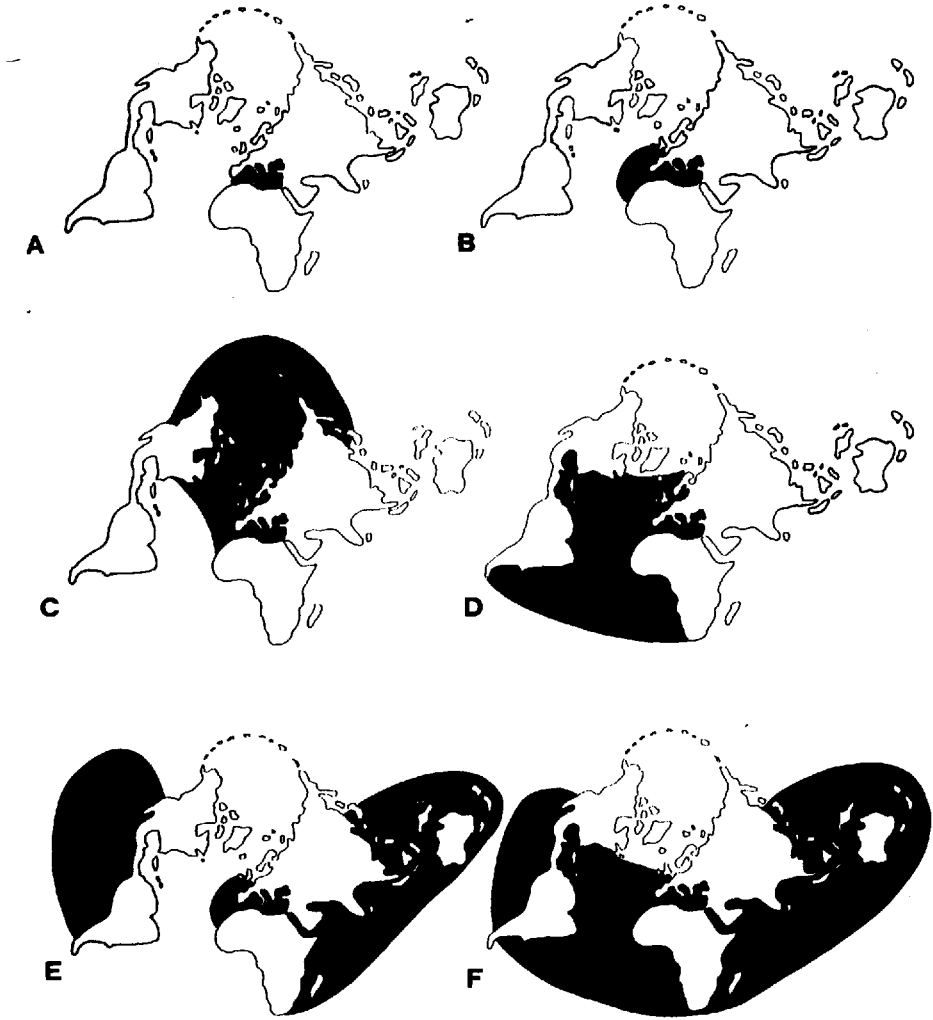


Figure 1. Zoogeographical regions for the Mediterranean hydromedusan fauna: A, Mediterranean-Endemic; B, Mediterranean-Atlantic; C, Boreal; D, Tropical-Atlantic; E, Indo-Pacific; F, Circumtropical; Cosmopolitan not shown. (Redrawn after C. N. Bianchi, unpublished.)

Trachymedusae). Almost half of the Mediterranean species, however, have lost the medusa stage by reduction (Table 1), so that a much varied array of dispersal strategies is present in this group. In this paper we consider the planktonic medusa as the sexual, adult stage: it releases the gametes, giving rise to non-feeding planula larvae from which, in most cases, originate hydroids (a specialized type of larva) which, then, will produce medusae (see Boero & Bouillon, 1987; Boero & Sarà, 1987; and Bouillon, Boero & Fraschetti, 1991, for recent discussions). This interpretation, however, is not accepted by other hydromedusan workers (Cornelius, 1990). When the medusa is present in the cycle, the adult shows the highest vagility and could be considered as the main agent of dispersal. This is a reversal of the 'norm' in meroplanktonic animals, where the larva, and not the adult, has a planktonic life.

TABLE 1. Distribution of Mediterranean hydromedusae

	<i>T</i>	%	<i>m</i>	%	<i>g</i>	%	<i>mg</i>	%
Endemic	67	19.4	35	52.2	28	41.7	4	5.9
Mediterranean Atlantic	40	11.3	18	46.1	22	53.8	—	—
Boreal	45	13.3	16	36.9	27	58.6	2	4.3
Tropical Atlantic	41	11.8	22	53.6	19	46.3	—	—
Indo-Pacific	28	8.0	†22	78.6	6	21.4	—	—
Circumtropical	71	20.5	†53	74.6	17	23.9	1	1.4
Cosmopolitan	43	12.4	†16	34.8	26	62.7	1	2.3
Non-classifiable	11	3.2	6	54.5	3	27.2	2	18.1
Total	346		188	54.3	148	42.7	10	2.9

T, Total number of species referable to a given contingent and %, percentage of that contingent in respect to the total fauna; *m*, number of species with medusa and %, percentage of such species within the contingent; *g*, number of species with fixed gonophores and %, percentage of such species within the contingent; *mg*, number of species with liberable eumedusoids and %, percentage of such species within the contingent. *, Significant difference (χ^2 test, $P < 0.05$) between species with medusae and species with fixed gonophores or liberable eumedusoids; † same difference, but highly significant ($P < 0.01$).

Types of hydromedusan life cycle and their possible relevance to dispersal
(Fig. 2)

(1) *Medusa – planula – benthic hydroid – medusa*

Dispersal is dependent on several factors: duration of life of the medusa (from a few days to several months), duration of the free life of the usually hollow and floating coeloblastula and planula larva (too few data for generalization, but a maximum of 15 days seems to be possible), dispersal of hydroid via planktonic propagules (e.g. *Halecium pusillum*), life on nectonic (*Hydrichthys*), or planktonic (*Obelia*, *Kinetocodium*, *Pelagiana*, parasitic Narcomedusae etc.) organisms, and settling on floating algae or objects. A particular case is that recently reported by Bouillon *et al.* (1991) in *Laodicea indica*, a leptomedusa producing planulae which, according to the season, can give rise to hydroid colonies or short-lived fixed gonothecae which immediately release a single medusa.

(2) *Liberated eumedusoid or swimming gonophore – planula – benthic hydroid – liberated eumedusoid or swimming gonophore*

The planktonic life of liberated eumedusoids or swimming gonophores (re-evolved medusiform stages) is usually just a few hours (see Boero & Bouillon, 1989) limiting the extent of dispersal. As in the former cases, however, the hydroid can contribute to dispersal.

(3) *Benthic hydroid – planula – benthic hydroid*

The coeloblastula is absent and the morula and planula stages of these species are usually dense and tend to sink. The possibilities for dispersal are thus limited. In a few species the planula is known to be linked to the mother colony by mucous threads which break only when settlement occurs. In some groups a non-feeding actinula larva occurs, showing some possibilities of dispersal. Production of asexual propagules, life on pelagic organisms or on floating objects, are still possible.

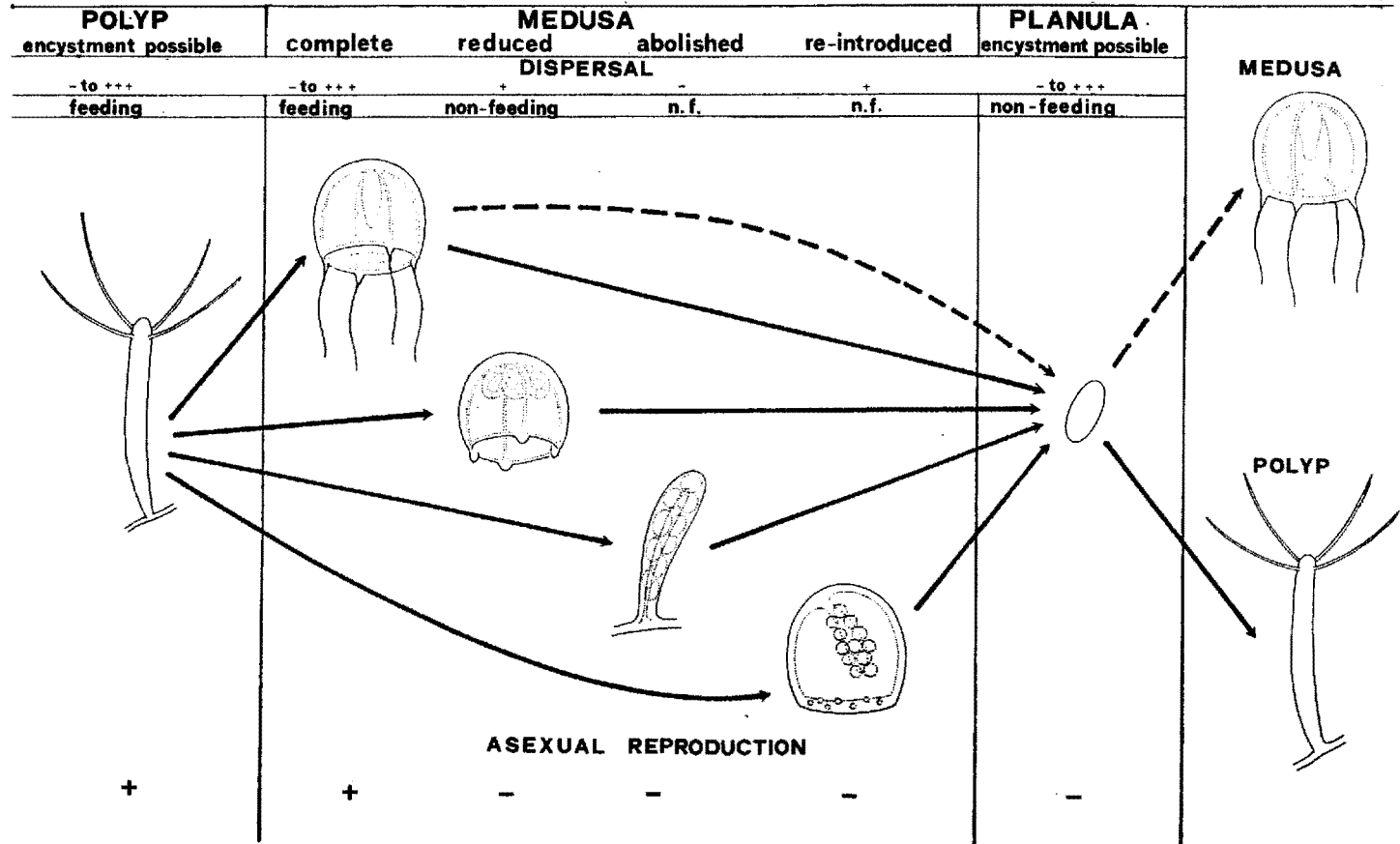


Figure 2. Life-cycle patterns of hydromedusae, with dispersal possibilities (from - to + + +), presence (+) or absence (-) of asexual reproduction, and trophic value of the various stages. Broken arrows: direct development, with no hydroid stage; solid arrows: indirect development, with hydroid stage.

(4) *Medusa – planula – planktonic hydroid – medusa*

The benthic life is abolished and different dispersal strategies are employed by planula, hydroid and medusa stages (e.g. *Margelopsis*, *Pelagohydra*, *Velella*, *Porpita*, *Climacocodon*, *Eirene hexanemalis*).

(5) *Medusa – planula – medusa*

This is considered a primitive type of life cycle and it is characteristic of most of the Narcomedusae and all Trachymedusae. Besides exceptional benthic forms (*Ptychogastria*), all species are holoplanktonic.

Asexual reproduction of medusae

The life span of medusae should set a limit on their dispersive capabilities. But this is compensated by several ways of asexual reproduction such as fission and budding of medusae from the manubrium or tentacular bulbs, gonothecae on the circular or radial canals, polyps on the manubrium or radial canals. In this way a medusa and its offspring should be able to cover unlimited distances, provided that food availability and chemico-physical features of the water are suitable (Kramp, 1959; Bouillon *et al.*, 1986; Mills, 1987).

Encystment

Almost all hydroids are able to produce resting stages represented by dormant hydrorhizae (Calder, 1990). Several species are known to produce planula encystment and this phenomenon is probably more widespread than is known. Recently Carré & Carré (1990) have described the asexual formation of resting frustules from the medusa of *Eucheilota paradoxica*. Specimens capable of such encystments can survive for long periods and become active again under proper conditions. When the possibility of hydroids settling on floating objects (including ships) is considered, it is evident that, theoretically, dispersal has no limit (Cornelius, 1981; Jackson, 1986).

These life-cycle patterns should generate different dispersal possibilities, so that it might be possible to classify them along an efficiency-of-dispersal gradient. Picard (1958) and Boero (1984), however, have remarked that life-cycle features seem unimportant in determining the distribution patterns of hydromedusae.

The most efficient cycle for dispersal we could envisage *a priori* is one with both medusa and benthic hydroid. The two completely different dispersal and feeding strategies, plus the planula stage, enable a wide array of possibilities, even though not all species presumably can express the maximum theoretical dispersal potential. The cycle of *Laodicea indica*, with the possibility of shifting from benthic hydroid to benthic gonotheca, can be placed in this category. It might be expected that species with such a life cycle would show a low rate of endemism, with a high tendency to wide distribution.

The second position might be held by species having free medusae and planktonic hydroids. They cannot take advantage of settlement and encystment on floating objects, but are anyway able to disperse with two morphs having different dispersal and feeding strategies.

Holoplanktonic species, with the medusa stage only, rely on a single morph which, however, has no limitation due to the finding of a proper substratum for

larval settlement. The possibility of resting stages is only hypothetical and their distribution is limited by food availability and physico-chemical conditions.

The lowest vagility is shown by species with liberable eumedusoids, swimming gonophores and, above all, fixed gonophores. Their dispersal is mainly due to the planula displacement but since their larval stages are solid and usually non-floating, the covered distances should not be relevant. The dispersal of propagules and resting stages deriving from the hydroid, however, is still theoretically rather high.

We are aware that this scenario is oversimplified. The general biology of the great majority of the species is still unknown and, furthermore, the life cycles of about 75% of the species are still to be elucidated. It is to be expected that species with no medusa stages show a greater tendency to dispersal by asexual propagules or simply by colony rafting, but it is also true that species with medusae can show planula settlement on substrata such as pteropods, fishes etc., so that there should be a certain balance among the different dispersal mechanisms.

We will try to test the preceding assumptions against the known distribution of the Mediterranean hydromedusae, assigning them to zoogeographical groups and considering their life cycles. The analysis will be hindered by incomplete knowledge of distributions and also by the fact that some areas have been extensively investigated for medusae but not for hydroids, and vice versa.

It has been impractical to build up a group for each category of life cycle, and we choose to divide the species into forms with medusae, forms with fixed gonophores, and forms with liberable eumedusoids or swimming gonophores. Species with pelagic hydroids and Trachymedusae (with no hydroid stage) constitute a small fraction of the whole fauna: for ease of analysis they have been considered as species with both hydroid and medusa stages.

Until now all species of hydromedusae are supposed to have a polyp stage, with the exception only of some Narcomedusae and the Trachymedusae. But the life cycles of 82 of the 143 Antho- and Leptomedusae species with medusae are unknown or poorly known. As suggested by Bouillon *et al.* (1991) it could be that many or at least some species known only as medusae have no 'classical' polyp stage.

Thus our speculations are based on incomplete knowledge, but it is also true that the study of Mediterranean hydromedusae has been, and still is, rather intense and that the Mediterranean is one of the best known hydromedusan faunas of the world. The number of species treated here probably constitutes a sufficiently large sample to allow some general considerations. The knowledge of the distributions of many of them will surely improve, but this will take place slowly and this is not a sufficient reason to delay delineation of general aspects of species distribution.

The Mediterranean hydromedusan fauna

By hydromedusae we mean practically all Hydrozoa except Siphonophorae, that is: Antho-, Lepto-, Laingio-, Limno-, Narco- and Trachymedusae, and the Actinulidae (see Bouillon, 1985, for definition of orders).

No recent paper, to our knowledge, has treated the complete hydromedusan fauna of the Mediterranean. Kramp (1959, 1961) treated the medusa stage only

(65 species), and Picard (1958) considered both polyp and medusa stages of Antho- and Leptomedusae (191 species). The preparation of a monograph on Mediterranean hydromedusae has also contributed to the knowledge of the group. The only part to have been published is that on the Anthomedusae/Capitata (Brinckmann-Voss, 1970).

Many recent papers have greatly modified the knowledge of the composition of the hydromedusan fauna of the Mediterranean, with new records and descriptions of new families, genera, and species. These, at first, were considered endemic to the basin, but many have since been recorded from other seas and oceans.

MATERIAL AND METHODS

The distribution of the representatives of the various orders is summarized in Tables 1 and 2. With the χ^2 test we tested the significance of the difference in numbers between species with medusae and species with fixed gonophores, swimming gonophores and liberable eumedusoids.

We included the species with swimming gonophores or liberable eumedusoids in the group of species with fixed gonophores for a number of reasons: (1) the possibility could be high that there are more species of Leptomedusae liberating

TABLE 2. Distribution of the different orders of Mediterranean hydromedusae.

	<i>T</i>	%	<i>m</i>	%	<i>g</i>	%	<i>mg</i>	%
Anthomedusae								
Endemic	34	23.9	15	44.1	16	47.0	3	8.8
Mediterranean Atlantic	15	10.6	*11	73.3	4	26.6	—	—
Boreal	26	18.3	12	46.1	13	50.0	1	4.0
Tropical Atlantic	11	7.7	7	63.6	4	36.3	—	—
Indo-Pacific	12	8.4	*10	83.3	2	16.7	—	—
Circumtropical	34	23.9	†25	73.5	8	23.5	1	2.9
Cosmopolitan	5	3.5	1	20.0	4	80.0	—	—
Non-classifiable	5	3.5	4	80.0	1	20.0	—	—
Total	142	40.5	*85	59.9	52	36.6	5	3.5
Leptomedusae								
Endemic	24	16.1	11	45.8	12	50.0	1	4.1
Mediterranean Atlantic	21	12.9	†4	20.0	17	80.0	—	—
Boreal	18	11.6	†4	26.3	13	68.4	1	5.2
Tropical Atlantic	25	16.1	10	40.0	15	60.0	—	—
Indo-Pacific	12	7.7	8	66.6	4	33.3	—	—
Circumtropical	16	12.2	7	43.7	9	56.2	—	—
Cosmopolitan	33	20.0	†10	27.3	22	69.7	1	3.0
Non-classifiable	5	3.2	3	60.0	1	20.0	1	20.0
Total	154	44.5	†57	37.0	93	60.3	4	2.5
Anthomedusae-Leptomedusae								
Endemic	58	19.6	—	—	—	—	—	—
Mediterranean Atlantic	36	11.8	—	—	—	—	—	—
Boreal	44	15.2	—	—	—	—	—	—
Tropical Atlantic	36	12.1	—	—	—	—	—	—
Indo-Pacific	24	8.1	—	—	—	—	—	—
Circumtropical	50	16.9	—	—	—	—	—	—
Cosmopolitan	38	12.8	—	—	—	—	—	—
Non-classifiable	10	3.4	—	—	—	—	—	—
Total	296	85.5	—	—	—	—	—	—

TABLE 2. *contd.*

	<i>T</i>	%	<i>m</i>	%	<i>g</i>	%	<i>mg</i>	%
Limnomedusae								
Endemic	—	—	—	—	—	—	—	—
Mediterranean Atlantic	1	12.5	1	100	—	—	—	—
Boreal	1	12.5	—	—	1	100	—	—
Tropical Atlantic	2	22.2	2	100	—	—	—	—
Indo-Pacific	—	—	—	—	—	—	—	—
Circumtropical	3	37.5	3	100	—	—	—	—
Cosmopolitan	1	12.5	1	100	—	—	—	—
Non-classifiable	1	12.5	—	—	—	—	1	100
Total	9	2.6	*7	75	1	12.5	1	12.5
Narcomedusae (all <i>m</i>)								
Endemic	8	40	—	—	—	—	—	—
Mediterranean Atlantic	1	5	—	—	—	—	—	—
Boreal	—	—	—	—	—	—	—	—
Tropical Atlantic	—	—	—	—	—	—	—	—
Indo-Pacific	2	10	—	—	—	—	—	—
Circumtropical	8	40	—	—	—	—	—	—
Cosmopolitan	1	5	—	—	—	—	—	—
Non-classifiable	—	—	—	—	—	—	—	—
Total	20	5.8	—	—	—	—	—	—
Trachymedusae (all <i>m</i>)								
Endemic	1	5.9	—	—	—	—	—	—
Mediterranean Atlantic	1	5.9	—	—	—	—	—	—
Boreal	—	—	—	—	—	—	—	—
Tropical Atlantic	3	17.6	—	—	—	—	—	—
Indo-Pacific	1	5.9	—	—	—	—	—	—
Circumtropical	10	58.8	—	—	—	—	—	—
Cosmopolitan	1	5.9	—	—	—	—	—	—
Non-classifiable	—	—	—	—	—	—	—	—
Total	17	4.9	—	—	—	—	—	—
Actinulidae (all <i>g</i>)								
Cosmopolitan	2	66.7	—	—	—	—	—	—
Mediterranean Atlantic	1	33.3	—	—	—	—	—	—
Total	3	0.8	—	—	—	—	—	—
Laingiomedusae (all <i>m</i>)								
Indo-Pacific	1	100	—	—	—	—	—	—
Total	1	0.2	—	—	—	—	—	—

Abbreviations as in Table 1.

gonophores than hitherto thought (Boero & Bouillon, 1989); (2) some species may switch from fixed gonophores to liberable eumedusoids, according to environmental conditions, so the two possibilities are not mutually exclusive (Stefani, 1959); (3) the possibilities of dispersal obtained with a liberable eumedusoid are presumably more similar to those obtained with fixed gonophores than to those obtained with medusae.

RESULTS

The number of hydromedusan species recorded from the Mediterranean is 346 (see Appendix). The number of species with medusae is not statistically different

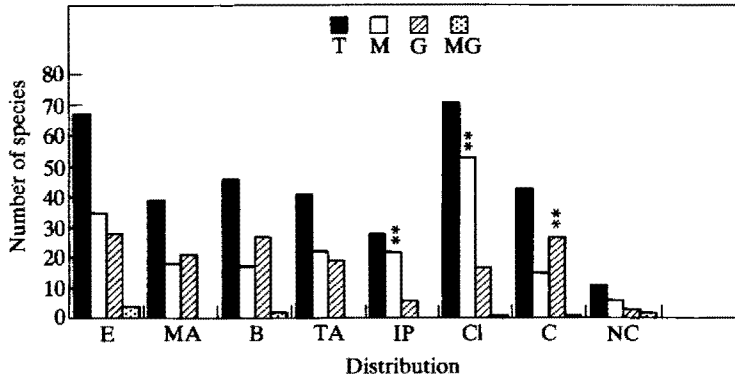


Figure 3. Species numbers of Mediterranean hydromedusae. E, Endemic; MA, Mediterranean-Atlantic; B, Boreal; TA Tropical-Atlantic; IP, Indo-Pacific; CI Circumtropical; C, Cosmopolitan; NC, non-classifiable. T, Total; M, species with medusa; G, species with fixed gonophores; MG, species with liberable eumedusoids or swimming gonophores; *, Significant difference (χ^2 test, $P < 0.05$) between species with medusae and species with fixed or swimming gonophores or liberable eumedusoids; **same difference, but highly significant ($P < 0.01$).

than that without medusae. The situation, however, is completely different when the most abundant groups are considered separately. Anthomedusae show a significant prevalence of species with medusae, whereas in Leptomedusae the species with fixed gonophores or short-lived medusoids prevail (Table 2).

The different zoogeographical groups (Figs 3–5) are treated separately in order of importance.

Circumtropical species

The circumtropical species are the most abundant, with a highly significant prevalence of species with medusae. The Anthomedusae show a highly significant difference in favour of the medusa stage; the Leptomedusae show no significant difference between species with and without medusae; all Limno-Narco- and Trachymedusae have a well-developed medusa stage. The data show that the medusa stage is dominant in the circumtropical Anthomedusae, but not in the Leptomedusae.

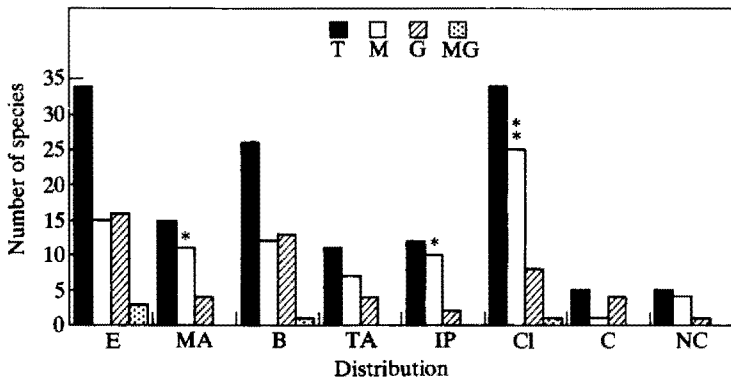


Figure 4. Species numbers of Mediterranean Anthomedusae. Key as in Fig. 3.

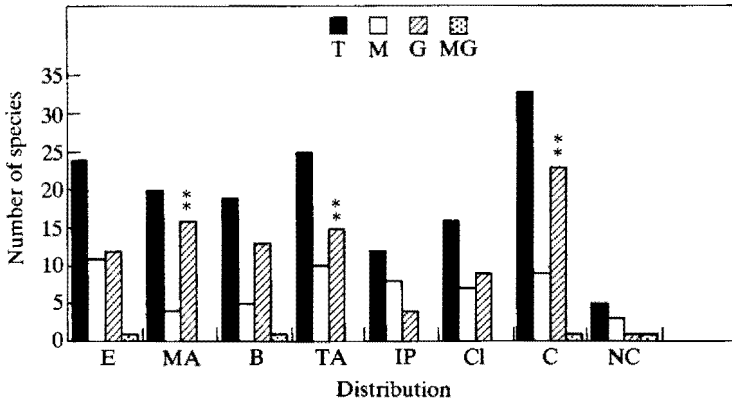


Figure 5. Species numbers of Mediterranean Leptomedusae. Key as in Fig. 3.

Endemic species

The endemic contingent is almost as important as the circumtropical one. There is no significant difference between species with and without medusae in Antho- and Leptomedusae. All Narco- and Trachymedusae have medusae. The presence of a medusa stage in the life cycle of endemic Mediterranean hydromedusae is rather widespread.

Boreal species

The overall difference between species with and without medusae is not statistically significant. Leptomedusae, however, show a statistically highly significant difference in favour of fixed gonophores. As in the circumtropical contingent, Antho- and Leptomedusae show differing life-cycle patterns, Anthomedusae being 'neutral', whereas Leptomedusae show a relevant reduction of the medusa stage. It is suggestive that the orders with prevalence of the medusa stage (Narco-, Trachymedusae) have no boreal representatives in the Mediterranean.

Cosmopolitan species

We reluctantly introduce this category which should comprise panoeanic species occurring from the Polar seas to the Equator. It is unlikely that such species really exist, and their records in the literature could be due to insufficient possibilities of discrimination in current taxonomy. Many of the supposed cosmopolitan species may turn out to be eurythermic circumtropical, but this sort of zoogeographical revision is outside the scope of the present paper.

The difference between cosmopolitan species with and without medusae is statistically highly significant in favour of fixed gonophores. Cosmopolitan Anthomedusae, however, show no significant difference whereas Leptomedusae show a highly significant difference for fixed gonophores; all Narco-, Limno- and Trachymedusae have medusae whereas the Actinulidae have fixed gonophores.

The Mediterranean species with the broadest distributions show a sharp

prevalence of forms deprived of the medusa stage and, again, Antho- and Leptomedusae behave in an opposite way.

Tropical-Atlantic species

There are no significant differences between species with and without medusae. This contingent does not show a significant prevalence of a given type of life cycle.

Mediterranean-Atlantic species

There is no overall significant difference between species with and without medusae. However, the Anthomedusae have a statistically significant difference in favour of the medusa stage and the Leptomedusae have a statistically highly significant difference in favour of fixed gonophores; Limno-, Narco- and Trachymedusae, all have medusae; the only representative of the Actinulidae has fixed gonophores. The presence of the medusa stage is different in Antho- and Leptomedusae, the two orders showing opposite life-cycle patterns. As in some of the preceding cases, this is compensated in the overall picture, so that the presence or absence of the medusa seems unimportant.

Indo-Pacific species

This group of species shows a highly significant difference in favour of the medusa stage. The difference, however, is not significant for Leptomedusae. The presence of a medusa stage in the life cycles is widespread in the Indo-Pacific species inhabiting the Mediterranean, but not in the Leptomedusae, in which the situation is balanced.

DISCUSSION

Affinities of the Mediterranean hydromedusan fauna

The endemic group is second only to the circumtropical one. This indicates a great originality of the Mediterranean fauna. As remarked by Picard (1958), however, the only certain endemics are those species restricted to particular habitats not available outside the Mediterranean. *Posidonia oceanica* meadows constitute an outstanding example (Boero, 1987). Many endemic species have been found only once, in spite of intense collection in the basin in recent decades. Their endemism could be due to incomplete knowledge of their distribution. These species could have arrived in the Mediterranean from other, less studied, areas where they are more abundant but still undetected. Some of the endemic species seem to be restricted to the Adriatic which, in fact, is a quite peculiar sea. Its conditions might have facilitated speciation.

The environmental conditions of the Mediterranean, as already mentioned, are very variable during the year and this should favour forms with a marked tendency towards seasonality, such as hydromedusae. Warm-water species can proliferate in the summer and pass the winter as resting stages. Cold-water species could be active in the winter and spend the summer as resting stages. This pattern is evident from studies of hydromedusae, of both hydroid and

medusa stages (see Boero, 1984, for a review, and Morri & Bianchi, 1983, for a discussion of brackish water species).

Some of the endemic species could be relicts of the Tethys Sea. This can apply to the species typical of *Posidonia* since this plant is supposed to be itself a Tethyan relict. *Paracoryne huvei* could be a Tethyan relict too, and features of its life cycle (Bouillon, 1975) could have enabled it to survive the Messinian crisis.

Not many other species are easily classifiable in their endemicity. As already said, they could be 'false endemics', due to sparse zoogeographical information, but they could also have originated in the Mediterranean after, or during, the Messinian crisis (see Pérès, 1985; Sarà, 1985; Tortonese, 1985; Por, 1989, for recent discussions). Some endemic species are of dubious taxonomic validity, owing to insufficient description. The difference in salinity between the Mediterranean and the Atlantic could play a role in the confinement of stenohaline species which evolved in the Mediterranean Sea. Dispersal of specimens settled on floating objects or of strictly shallow-water species could be influenced by the fact that, owing to the differences in density, the Atlantic water enters the Mediterranean basin from the surface, whereas the Mediterranean water flows out at a deeper level. Differences in salinity and features of circulation could be the main causes for the confinement of the species which evolved in the Mediterranean.

One hundred and twenty-six species are boreal, tropical Atlantic, or Mediterranean-Atlantic; and 114 species are circumtropical or cosmopolitan. Almost 70% of the hydromedusan fauna living in the Mediterranean could have entered through the Strait of Gibraltar, having been found in the corresponding part of the Atlantic and also elsewhere.

Indo-Pacific species are noteworthy, representing only 8.0% of the fauna. Picard (1958) stated that no Indo-Pacific species was present in the Mediterranean, but the studies of Schmidt (1973, 1976), Marinopulos (1979), Lakkis & Zeidane (1985), Goy, Lakkis & Zeidane (1990), Margulis (1989) and others have shown that certain Indo-Pacific species are present in the Mediterranean, mainly in the eastern part. This may be due to Lessepsian migration through the Suez Canal, even though the absence of information about the hydromedusan fauna of the Eastern Mediterranean before the opening of this waterway allows no comparison between the situation before and after the presence of a connection between the Mediterranean and the Red Sea.

The hydromedusan fauna of the Mediterranean, then, comprises a conspicuous Atlantic contingent which, presumably, is the result of colonization through the Strait of Gibraltar. A relatively high number of endemics gives originality to the fauna, but it is difficult to ascertain their geographical origin, even though some species could be Tethyan relicts. Lessepsian migration via the Suez canal is slowly bringing Indo-Pacific species into the basin and it is expected that this group will become increasingly reported in the near future, following better exploration of the Eastern Basin. For a detailed treatment of Lessepsian migration see Por (1989).

The importance of life-cycle features in the distribution of Mediterranean hydromedusae

The hypotheses resulting from our analysis of life-cycle features are only partly confirmed by our data. Circumtropical species show a prevalence of cycles with a medusa, but cosmopolitan species behave in exactly the opposite way and fixed

gonophores prevail over medusae. The endemic species should have shown a sharp tendency towards medusa suppression. This is true for the species living on *Posidonia* leaves, but the whole endemic hydromedusan fauna shows no significant difference between the two general types of life cycle. The data regarding the single orders are even more contradictory. The opposite patterns of dominance of species with and without medusae indicate that Anthomedusae show a sharp tendency to conserve the medusa stage, whereas most Leptomedusae have suppressed it. This could be explained by some differences in colony organization between thecate (leptomedusan) hydroids and athecate (anthomedusan) hydroids. Thecates often have highly integrated colonies, formed by a high number of small polyps, whereas athecates usually have bigger polyps and less integrated colonies. A sharp specialization of the hydroid stage could have led to its prevalence over the medusa stage in Leptomedusae. This assumption, however, is probably too simplistic and the problem calls for a deeper analysis which is outside the scope of the present paper. The presence of the medusa stage, and so high degree of vagility, seems not to be of importance in the patterns of distribution of the Mediterranean hydromedusae as already observed by Picard (1958). Cornelius (1981), analysing the distribution of boreal hydroids, found that two-thirds lacked a medusa stage, being, however, widely distributed in cooler parts of the northern hemisphere.

The tendency to medusa reduction is evident also in the present data on Mediterranean species of boreal affinity, whereas the species in other zoogeographical groups do not show this feature. Furthermore, even though not explicitly stated, it is apparent that Cornelius (1981) dealt mainly with records of the hydroid stage, and this may limit the general value of his assumptions.

Asking the question if a medusa stage is 'better' for dispersal than fixed gonophores is comparable to asking if planktotrophic larvae are more efficient for dispersal than lecithotrophic ones. Following a series of mathematical expressions Vance (1973: 351) summarized his results with this sentence: 'Planktotrophy is more efficient than lecithotrophy when planktonic food is abundant and planktonic predation is low, and lecithotrophy is more efficient when either or both of these conditions is reversed'. It is quite possible that during daily, lunar, seasonal, annual and pluriannual cycles environmental conditions might be successively better and worse for the different types of dispersal mechanisms available to the various species. Over geological time this should result in a uniform geographical distribution of nearly all marine species, regardless of their dispersal mechanisms. This has obviously not occurred (see van der Spoel, 1983, for discussion).

In our opinion the distribution of marine species or, at least, of hydromedusae does not depend on their modes of dispersal, but on their limits of environmental tolerance. It is possible that, in one of the many different ways listed above, hydromedusae can widely disperse in the various oceans and seas. The absence of a given species from a certain area may not depend on its not reaching it, but on its lack of adaptation to local conditions. Over short periods, however, the presence of a long-lived pelagic stage seems to be a successful mode of dispersal, as indicated by the predominance of species with medusae in the Indo-Pacific contingent that, presumably, is the result of a recent migration of species from the Red Sea to the Mediterranean.

CONCLUSIONS

Historical factors have undoubtedly been important in recruitment to the Mediterranean hydromedusan fauna. Species which entered the basin from the Strait of Gibraltar after the Messinian crisis largely determined the present day fauna, together with a set of palaeoendemisms of Tethyan origin. The peculiar conditions of the Mediterranean, then, led to speciation and neoendemism. This interpretation is in accordance with the one detected in the Mediterranean benthos by Fredj (1974) and in the Mediterranean plankton by Furnestin (1979).

This overall picture seems to reconcile quite well with the dispersal theory, but it is notable that the possession of theoretically more or less efficient means of dispersal seems not to be important in the determination of the distribution of the species. Recent migration from the Red Sea through the Suez Canal, however, shows that efficient dispersal has a great importance in short-term colonization of newly-available areas. Among Indo-Pacific forms, representing probable Lessepsian migrants, in fact, species with medusae are significantly more numerous than species with fixed gonophores, even though this is not true for Leptomedusae. Por (1981) proposed a Lessepsian Province in the Eastern part of the Mediterranean in direct contact with the Suez Canal, this Province being characterized by a high number of Indo-Pacific species which had migrated to the Mediterranean via the Suez Canal. The migration occurred in spite of temperature and salinity barriers. Dispersal can clearly play a major role in determining the distribution of marine species. The same can be said for environmental features. Lessepsian migrants colonized the Mediterranean because they were able to reach it and because they are adapted to live in a 'Mediterranean' environment. Efficiency of dispersal is important during the first stages of colonization (prevalence of species with medusa stage in the group which entered via Suez) but seems unimportant over geological time ('balanced' situation in the species which entered via Gibraltar). The theory of vicariance could possibly apply to the endemic species living on the leaves of *Posidonia*, but a comparison of the hydroids of Mediterranean and Australian *Posidonia* has still to be done. The two theories explaining biogeographical patterns can both be applied to subsets of the hydromedusan fauna of the Mediterranean. Climatic factors, however, play an important role in 'shaping' a given fauna. Recent advances in biogeography (vicariance and cladistic biogeographies) refer almost entirely to terrestrial florae and faunae. It is reasonable to assume that oceans and mountains are almost insurmountable barriers for many terrestrial forms, but the situation in the seas is completely different, and geographical barriers are probably much less important in determining speciation and distribution patterns of marine organisms. Fauchald (1984) rightly stated that, theoretically, any organism can reach any point in the world ocean, in spite of its 'history'. For these reasons we consider premature, for instance, the comparison of the well-known hydromedusan fauna of the western Mediterranean with that of the eastern Mediterranean or with that of deep waters of the basin: their data sets are simply not comparable. The same is true for comparisons of the hydromedusan fauna of the Mediterranean with those of the Red and the Black seas.

As remarked by Sarà (1985) the understanding of the causes of the

distributions of marine animals will be possible by taking into account not only historical aspects (theories of vicariance and of dispersal) but also the conditioning of the present-day environmental features. The statement by Strong (1983: 640); 'Until autecological facets of existence are understood, it is tenuous to infer much about synecological influences' is, in our opinion, applicable also to marine zoogeography in terms of distribution of single species vs composition of regional faunas.

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APPENDIX

List of hydromedusan species hitherto recorded from the Mediterranean Sea. g: fixed gonophores; m: medusae; mg: liberable medusoids or swimming gonophores; ?: life cycle unknown or poorly known; E: endemic; MA: Mediterranean Atlantic; B: boreal; TA: Tropical Atlantic; IP: Indo-Pacific; CT: circumtropical; C: cosmopolitan; nc: non classifiable. Species marked with an asterisk (*) were added to the list when the present paper was in press and have not been considered in the text. The adopted classification reflects suggestions recently proposed in the paper by Bouillon *et al.* (1992).

Class HYDROZOA

Subclass HYDROIDOMEDUSAE

Order ANTHOMEDUSAE 142: 85 m, 52 g, 5 mg

Suborder Filifera

Superfamily Bougainvilloidea

Bougainvilliidae 20: 11 m, 9 g

<i>Bimeria vestita</i> Wright, 1859	C	g
(*) <i>Bougainvillia aurantiaca</i> Bouillon, 1980	IP	m
<i>Bougainvillia britannica</i> (Forbes, 1841)	B	m
<i>Bougainvillia maniculata</i> Haeckel, 1864	E	m?
<i>Bougainvillia multicilia</i> (Haeckel, 1879)	MA	m
<i>Bougainvillia muscus</i> (Allman, 1863)	CT	m
<i>Bougainvillia platygaster</i> (Haeckel, 1879)	TA	m?
<i>Clavopsella michaeli</i> (Berrill, 1948)	TA	g
<i>Dicoryne conferta</i> (Alder, 1857)	B	g
<i>Dicoryne conybeari</i> (Allman, 1864)	B	g
<i>Garveia franciscana</i> (Torrey, 1902)	CT	g
<i>Garveia grisea</i> Motz-Kossowska, 1905	E	g
<i>Garveia nutans</i> (Wright, 1859)	B	g
<i>Koellikerina fasciculata</i> (Péron & Lesueur, 1810)	MA	m
<i>Lizzia blondina</i> Forbes, 1848	B	m
<i>Lizzia fulgurans</i> (A. Agassiz, 1865)	nc	m?
<i>Lizzia octostyla</i> (Haeckel, 1879)	E	m?
<i>Nubiella mitra</i> Bouillon, 1980	IP	m?
<i>Pachycordyle napolitana</i> Weismann, 1883	TA	g
<i>Rhizorhagium arenosum</i> (Alder, 1862)	B	g
<i>Thamnostoma dibalium</i> (Busch, 1851)	E	m?

Cytaeidae 6: 4 m, 2 g

<i>Cytaeis pusilla</i> Gegenbaur, 1857	E	m?
<i>Cytaeis tetrastyla</i> Eschscholtz, 1829	CT	m?
<i>Cytaeis vulgaris</i> Agassiz & Mayer, 1899	IP	m?
<i>Paracytaeis octomia</i> Bouillon, 1981	IP	m?
<i>Perarella propagulata</i> Bavestrello, 1987	E	g
<i>Perarella schneideri</i> (Motz-Kossowska, 1905)	E	g

Superfamily Clavoidae

Clavidae 7: 2 m, 5 g

<i>Clava multicornis</i> (Forskål, 1775)	B	g
<i>Cordylophora caspia</i> (Pallas, 1771)	C	g
<i>Cordylophora pusilla</i> Motz-Kossowska, 1905	E	g

<i>Corydendrium parasiticum</i> (L., 1767)	CT	g
<i>Merona cornucopiae</i> (Norman, 1864)	CT	g
<i>Oceania armata</i> Koelliker, 1853	CT	m?
<i>Turritopsis nutricula</i> McCrady, 1859	CT	m

Superfamily Eudendrioidea

Eudendriidae 13: 13 g

<i>Eudendrium armatum</i> Tichomirowf, 1887	E	g
<i>Eudendrium calceolatum</i> Motz-Kossowska, 1905	E	g
<i>Eudendrium capillare</i> Alder, 1856	C	g
<i>Eudendrium carneum</i> Clarke, 1882	CT	g
<i>Eudendrium cuminghami</i> Kirkpatrick, 1910	TA	g
<i>Eudendrium fragile</i> Motz-Kossowska, 1905	E	g
<i>Eudendrium glomeratum</i> Picard, 1952	?CT	g
<i>Eudendrium merulum</i> Watson, 1985	IP	g
<i>Eudendrium motzkossowskiae</i> Picard, 1952	TA	g
<i>Eudendrium racemosum</i> (Gmelin, 1791)	IP	g
<i>Eudendrium rameum</i> (Pallas, 1766)	B	g
<i>Eudendrium ramosum</i> (L., 1758)	C	g
<i>Myrionema amboinense</i> Pictet, 1893	CT	G

Superfamily Hydractinoidea

Hydractiniidae 14: 8 m, 3 g, 3 mg

<i>Hydractinia aculeata</i> (Wagner, 1833)	E	mg
<i>Hydractinia echinata</i> Fleming, 1828	B	g
<i>Hydractinia fucicola</i> (M. Sars, 1857)	MA	g
<i>Hydractinia ornata</i> Bonnevie, 1899	B	mg
<i>Hydractinomma pruvoti</i> (Motz-Kossowska, 1905)	E	mg
<i>Podocoryne areolata</i> (Alder, 1862)	MA	m
<i>Podocoryne borealis</i> (Mayer, 1900)	B	m
<i>Podocoryne carnea</i> M. Sars, 1846	C	m
<i>Podocoryne exigua</i> (Haeckel, 1879)	E	m?
<i>Podocoryne hartlaubi</i> Neppi & Stiasny, 1911	MA	m
<i>Podocoryne minima</i> (Trinci, 1903)	MA	m?
<i>Podocoryne minula</i> (Mayer, 1900)	nc	m?
<i>Stylactaria inermis</i> (Allman, 1872)	E	g
<i>Tregoubovia atentaculata</i> Picard, 1958	E	m?

Ptilocodiidae 1: 1 g

<i>Thecocoedium brieni</i> Bouillon, 1967	MA	g
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Rhysiidae 1: 1 g

<i>Rhysia halecii</i> (Hickson & Gravely, 1907)	nc	g
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Stylasteridae 1: 1 g

<i>Errina aspera</i> (L., 1767)	E	g
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Superfamily Pandeoidea

Niobiidae 1: 1 m

<i>Niobia dendrotentaculata</i> Mayer, 1900	CT	m?
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Calyropsidae 2: 2 m

<i>Bythotiara murrayi</i> Gunther, 1903	CT	m?
<i>Calyropsis simplex</i> Kramp & Damas, 1925	TA	m?

Pandeidae 13: 13 m

<i>Amphinema dinema</i> (Péron & Lesueur, 1810)	CT	m
<i>Amphinema rubrum</i> (Kramp, 1957)	nc	m?
<i>Amphinema rugosum</i> (Mayer, 1900)	CT	m
<i>Amphinema turrida</i> (Mayer, 1900)	CT	m?
<i>Leuckartiara nobilis</i> Hartlaub, 1913	B	m?
<i>Leuckartiara octona</i> (Fleming, 1823)	CT	m
<i>Merga galleri</i> Brinckmann, 1962	E	m
<i>Merga tergostina</i> (Neppi & Stiasny, 1912)	IP	m
<i>Merga tregoubovi</i> Picard, 1960	IP	m?
<i>Merga violacea</i> (Agassiz & Mayer, 1899)	CT	m?
<i>Neoturris pileata</i> (Forsk., 1775)	TA	m
<i>Octotiara russelli</i> Kramp, 1953	IP	m
<i>Pandea conica</i> (Quoy & Gaimard, 1827)	CT	m

	Protiaridae 2: 2 m		
<i>Halitiara formosa</i> Fewkes, 1882		CT	m?
(* <i>Halitiara inflexa</i> Bouillon, 1980		IP	m
<i>Protiaira tetranema</i> (Pefon & Lesucur, 1810)		MA	m?
	Trichydridae 1: 1 m		
<i>Trichydra oligonema</i> (Kramp, 1955)		nc	m?
	Superfamily Rathkeoidea		
	Rathkeidae 1: 1 m		
<i>Rathkea octopunctata</i> (M. Sars, 1835)		B	m
	Suborder Capitata		
	Superfamily Acauloidea		
	Acaulidae 1: 1 g		
<i>Acauloides ilonae</i> (Brinckmann-Voss, 1965)		E	g
	Superfamily Corynoidea		
	Cladonematidae 1: 1 m		
<i>Cladonema radiatum</i> Dujardin, 1843		CT	m
	Corynidae 18: 12 m, 6 g		
<i>Coryne caespes</i> Allman, 1871		E	g
<i>Coryne epizoica</i> Stechow, 1921		E	g
<i>Coryne fucicola</i> De Filippi, 1866		E	g
<i>Coryne muscoides</i> (L., 1761)		MA	g
<i>Coryne pusilla</i> Gaertner, 1774		B	g
<i>Coryne pintneri</i> Schneider, 1897		E	g
<i>Dicodonium adriaticum</i> Graeffe, 1884		E	m?
<i>Dicodonium ocellatum</i> (Busch, 1851)		E	m?
<i>Dipurena dolichogaster</i> (Haeckel, 1864)		E	m?
<i>Dipurena halterata</i> (Forbes, 1846)		CT	m
<i>Dipurena ophiogaster</i> (Haeckel, 1879-80)		CT	m
<i>Dipurena reesi</i> Vannucci, 1956		TA	m
<i>Sarsia eximia</i> (Allman, 1859)		CT	m
<i>Sarsia gemmifera</i> Forbes, 1848		TA	m
<i>Sarsia producta</i> (Wright, 1858)		TA	m
<i>Sarsia prolifera</i> Forbes, 1848		MA	m?
<i>Sarsia tubulosa</i> (M. Sars, 1835)		B	m
	Eleutheriidae 3: 3 m		
<i>Eleutheria claparedi</i> Hartlaub, 1889		MA	m
<i>Eleutheria dichotoma</i> Quatrefages, 1842		B	m
<i>Staurocladia portmanni</i> Brinckmann, 1964		E	m
	Superfamily Moerisioida		
	Moerisiidae 5: 5 m		
<i>Moerisia carinae</i> Bouillon, 1981		IP	m
<i>Moerisia inkermanica</i> Paltschikowa-Ostroumova, 1925		IP	m
<i>Moerisia lyonsi</i> Boulenger, 1908		E	m
<i>Moerisia pallasii</i> (Derzhavin, 1912)		E	m
<i>Odesia maotica</i> (Ostroumoff, 1896)		MA	m
	Protohydridae 1: 1 g		
<i>Protohydra leuckarti</i> Greef, 1869		B	g
	(* <i>Spaerocorynidae</i>		
(* <i>Spaerocoryne bedoti</i> Pictet 1893		CT	m
	Superfamily Tricyclusoidea		
	Tricyclusidae 1: 1 g		
<i>Tricyclusa singularis</i> (Schulze, 1876)		B	g
	Superfamily Tubularioidea		
	Boreohydridae 1: 1 g		
<i>Psammohydra nana</i> Schultz, 1950		B	g

Corymorphidae 9: 8 m, 1 g

<i>Branchiocerianthus italicus</i> Stechow, 1923	E	g
<i>Corymorpha nutans</i> M. Sars, 1835	B	m
<i>Eucodonium brownei</i> Hartlaub, 1907	MA	m?
<i>Euphysora annulata</i> Kramp, 1928	IP	m?
<i>Euphysora bigelowi</i> Maas, 1905	CT	m
<i>Hybocodon prolifer</i> L. Agassiz, 1862	B	m
<i>Paragothea bathybia</i> Kramp, 1942	TA	m?
<i>Plotocnide borealis</i> Wagner, 1885	B	m?
<i>Vannuccia forbesii</i> (Mayer, 1894)	CT	m

Euphysidae 2: 1 m, 1 g

<i>Euphysa aurata</i> Forbes, 1848	B	m
(*) <i>Euphysa flammea</i> (Linko, 1905)	C?	m
<i>Siphonohydra adriatica</i> Salvini-Plawen, 1966	MA	g

Halocordylidae 1: 1 mg

<i>Halocordyle disticha</i> (Goldfuss, 1820)	CT	mg
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Paracorynidae 1: 1 g

<i>Paracoryne huwei</i> Picard, 1957	E	g
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Tubulariidae 9: 6 m, 3 g

<i>Ectopleura dumortieri</i> (Van Beneden, 1844)	CT	m
<i>Ectopleura minerva</i> Mayer, 1900	CT	m?
<i>Ectopleura sacculifera</i> Kramp, 1957	CT	m?
<i>Ectopleura wrightii</i> Petersen, 1979	E	m
<i>Eugothoea petalina</i> Margulis, 1989	E	m?
<i>Rhabdoon singularis</i> Keferstein & Ehlers, 1861	IP	m?
<i>Tubularia crocea</i> Agassiz, 1862	CT	g
<i>Tubularia indivisa</i> L., 1758	B	g
<i>Tubularia larynx</i> Ellis & Solander, 1786	B	g

Superfamily Porpitoidea

Porpitidae 2: 2 m

<i>Porpita porpita</i> (L., 1758)	CT	m
<i>Velella velella</i> (L., 1758)	CT	m

Superfamily Zancleoidae

Cladocorynidae 1: 1 g

<i>Cladocoryne floccosa</i> Rotch, 1871	CT	g
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Halocorynidae 1: 1 mg

<i>Halocoryne epizoica</i> Hadzi, 1917	E	mg
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Rosalindidae 1: 1 m

<i>Rosalinda incrustans</i> (Kramp, 1947)	B	m?
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Zancleidae 2: 2 m

<i>Zanclea costata</i> Gegenbaur, 1857	CT	m
<i>Zanclea sessilis</i> (Gosse, 1853)	MA	m

Order LEPTOMEDUSAE 154: 57 m, 93 g, 4 mg

Suborder **Conica**

Infraorder Campanulinida

Superfamily Campanulinoidea

Aequoreidae 4: 4 m

<i>Aequorea forskalea</i> Péron & Lesueur, 1810	CT	m
<i>Aequorea conica</i> Browne, 1905	IP	m?
<i>Aequorea pensilis</i> (Eschscholtz, 1829)	IP	m?
<i>Zygocanna</i> sp. Babnik, 1948	nc	m?

Blackfordiidae 1: 1 m

<i>Blackfordia virginica</i> Mayer, 1910	B	m
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	Campanulinidae 4: 4 g	B	g
<i>Calycella syringa</i> (L., 1767)		B	g
<i>Campanulina hincksii</i> Hartlaub, 1897		IP	g
<i>Egmondella amirantensis</i> Millard & Bouillon, 1973		B	g
<i>Lafoeina tenuis</i> G.O. Sars, 1874			
	Malagazziidae 1: 1 m	MA	m?
<i>Octophialucium funerarium</i> (Quoy & Gaimard, 1827)			
	Phialellidae 1: 1 m	C	m
<i>Phialella quadrata</i> (Forbes, 1848)			
	Superfamily Dipleurosomatoidea		
	Melicertidae 1: 1 m	E	m?
<i>Orchistomella graeffei</i> (Neppi & Stiasny, 1911)			
	Orchistomidae 1: 1 m	E	m?
<i>Orchistoma agariciforme</i> Keller, 1884			
	Superfamily Eirenoidea		
	Eirenidae 9: 8 m 1 mg	IP	m
<i>Eirene viridula</i> (Péron & Lesueur, 1810)		E	mg
<i>Eugymnanthea inquilina inquilina</i> Palombi, 1935		CT	m
<i>Eutima gegenbauri</i> (Haeckel, 1864)		TA	m
<i>Eutima gracilis</i> (Forbes & Goodsir, 1853)		CT	m
<i>Eutima mira</i> McCrady, 1859		MA	m?
<i>Eutonina scintillans</i> (Bigelow, 1909)		MA	m?
<i>Helgicirrha cari</i> (Haeckel, 1864)		TA	m?
<i>Helgicirrha schulzei</i> Hartlaub, 1909		TA	m
<i>Neotima lucullana</i> (Delle Chiaje, 1822)		E	m?
	Superfamily Laodiceoidea		
	Laodiceidae 8: 8 m	TA	m?
<i>Krampella dubia</i> Russell, 1957		E	m?
<i>Laodicea bigelowi</i> Neppi & Stiasny, 1912		IP	m?
<i>Laodicea fijiana</i> Agassiz & Mayer, 1899		E	m?
<i>Laodicea ocellata</i> Babnik, 1948		TA	m?
<i>Laodicea neptuna</i> Mayer, 1900		TA	m?
<i>Laodicea undulata</i> (Forbes & Goodsir, 1851)		E	m?
<i>Melicertissa adriatica</i> Neppi, 1915		C	m
<i>Staurophora mertensii</i> Brandt, 1838			
	Tiarannidae 1: 1 m	C	m
<i>Mooderia rotunda</i> (Quoy & Gaimard, 1827)			
	Tiaropsiidae 2: 2 m	E	m?
<i>Octogonade mediterranea</i> Zoja, 1896		E	m
<i>Tiaropsidium mediterraneum</i> (Metschnikoff, 1886)			
	Superfamily Lovenelloidea		
	Cirrholoveniidae 1: 1 m	IP	m?
<i>Cirrholovenia tetranema</i> Kramp, 1959			
	Eucheilotidae 3: 3 m	E	m?
<i>Eucheilota maasi</i> Neppi & Stiasny, 1911		nc	m
<i>Eucheilota paradoxica</i> Mayer, 1900		C	m?
<i>Eucheilota ventricularis</i> McCrady, 1859			
	Lovenellidae 5: 5 m	nc	m
<i>Lovenella chiquitita</i> Millard, 1959		TA	m?
<i>Lovenella cirrata</i> (Haeckel, 1879)		MA	m
<i>Lovenella clausa</i> (Lovén, 1836)		B	m?
<i>Lovenella gracilis</i> (Clarke, 1882)		B	m?
<i>Lovenella paniculata</i> (G. O. Sars, 1873)			
	Superfamily Mitrocomioidea		
	Mitrocomidae 2: 2 m	E	m
<i>Mitrocoma annae</i> Haeckel, 1864		MA	m?
<i>Mitrocomella brownei</i> (Kramp, 1930)			

Infraorder Lafoeida

Superfamily Lafoeidea

Hebellidae 7: 4 m, 2 g, 1 mg

<i>Hebella brochi</i> (Hadzi, 1913)	E	m?
<i>Hebella furax</i> Millard, 1957	TA	m?
<i>Hebella parasitica</i> (Ciamician, 1880)	nc	mg
<i>Hebella scandens</i> (Bale, 1888)	C	m?
<i>Hebella urceolata</i> Millard, 1964	TA	m?
<i>Scandia gigas</i> (Pieper, 1884)	B	g
<i>Scandia michael-sarsi</i> (Leloup, 1935)	TA	g

Lafoeidae 6: 6 g

<i>Acryptolaria conferta</i> (Allman, 1877)	C	g
<i>Filellum serpens</i> (Hassall, 1848)	C	g
<i>Filellum serratum</i> (Clarke, 1879)	C	g
<i>Lafaea dumosa</i> (Fleming, 1820)	C	g
<i>Lafaea fruticosa</i> (Sars, 1851)	C	g
<i>Zygophylax biarmata</i> Billard, 1905	C	g

Infraorder Haleciida

Superfamily Halecioidea

Haleciidae 18: 1 m, 16 g, 1 mg

<i>Campalecium medusiferum</i> Torrey, 1902	IP	m?
<i>Halecium banyulense</i> Motz-Kossowska, 1911	E	g
<i>Halecium beanii</i> (Johnston, 1838)	C	g
<i>Halecium conicum</i> Stechow, 1919	E	g
<i>Halecium halecinum</i> (L., 1758)	C	g
<i>Halecium labrosum</i> Alder, 1859	B	g
<i>Halecium lankesteri</i> (Bourne, 1890)	TA	g
<i>Halecium mediterraneum</i> Weismann, 1883	MA	g
<i>Halecium muricatum</i> (Ellis & Solander, 1786)	B	g
<i>Halecium nanum</i> Alder, 1859	TA	g
<i>Halecium petrosium</i> Stechow, 1919	MA	g
<i>Halecium pusillum</i> (M. Sars, 1857)	TA	g
<i>Halecium sessile</i> Norman, 1867	C	g
<i>Halecium tenellum</i> Hincks, 1861	C	g
<i>Hydranthea aloysii</i> (Zoja, 1893)	E	g
<i>Hydranthea margarica</i> (Hincks, 1863)	B	mg
<i>Ophiodissa caciniiformis</i> (Ritchie, 1907)	CT	g
<i>Ophiodissa mirabilis</i> (Hincks, 1868)	MA	g

Infraorder Plumulariida

Superfamily Plumularoidea

Aglaopheniidae 15: 15 g

<i>Aglaophenia acacia</i> Allman, 1883	TA	g
<i>Aglaophenia elongata</i> Meneghini, 1845	MA	g
<i>Aglaophenia harpago</i> Von Schenck, 1963	E	g
<i>Aglaophenia kirchenpaueri</i> (Heller, 1868)	MA	g
<i>Aglaophenia latecarinata</i> Allman, 1877	MA	g
<i>Aglaophenia lophocarpa</i> Allman, 1877	TA	g
<i>Aglaophenia picardi</i> Svoboda, 1979	E	g
<i>Aglaophenia pluma</i> (L., 1758)	C	g
<i>Aglaophenia octodonta</i> (Heller, 1868)	MA	g
<i>Aglaophenia tubiformis</i> (Marktanner-Turneretscher, 1890)	MA	g
<i>Aglaophenia tubulifera</i> (Hincks, 1861)	MA	g
<i>Cladocarpus dollfusi</i> Billard, 1924	MA	g
<i>Thecocarpus distans</i> (Allman, 1877)	B	g
<i>Thecocarpus myriophyllum</i> (L., 1758)	C	g
<i>Thecocarpus phyteuma</i> (Kirchenpauer, 1876)	B	g

Halopteridae 7: 7 g

<i>Antennella secundaria</i> (Gmelin, 1791)	C	g
<i>Antennella siliquosa</i> (Hincks, 1877)	MA	g
<i>Halopteris catharina</i> (Johnston, 1833)	C	g

<i>Halopteris diaphana</i> (Heller, 1868)	CT	g
<i>Halopteris glutinosa</i> (Lamouroux, 1816)	CT	g
<i>Halopteris liechtensterni</i> (Marktanner-Turneretscher, 1890)	E	g
<i>Schizotricha frutescens</i> (Ellis & Solander, 1786)	TA	g

Kirchenpaueriidae 3: 3 g

<i>Kirchenpaueria echinulata</i> (Hincks, 1868)	MA	g
<i>Kirchenpaueria pinnata</i> (L., 1758)	TA	g
<i>Ventromma haleciooides</i> (Alder, 1859)	C	g

Plumulariidae 7: 7 g

<i>Nemertesia antennina</i> (L., 1758)	C	g
<i>Nemertesia ramosa</i> Lamouroux, 1816	TA	g
<i>Nemertesia tetrasticha</i> (Meneghini, 1845)	E	g
<i>Plumularia obliqua</i> (Thompson, 1844)	CT	g
<i>Plumularia pulchella</i> Bale, 1882	IP	g
<i>Plumularia setacea</i> (L., 1758)	C	g
<i>Plumularia syriaca</i> Billard, 1930	E	g

Superfamily Sertularioidea

Sertulariidae 22: 22 g

<i>Amphisbetia operculata</i> (L., 1758)	B	g
<i>Diphasia margareta</i> (Hassall, 1841)	MA	g
<i>Dynamena disticha</i> (Bosc, 1802)	C	g
<i>Salacia desmoides</i> (Torrey, 1902)	MA	g
<i>Salacia dubia</i> (Billard, 1922)	MA	g
<i>Sertularella arbuscula</i> (Lamouroux, 1816)	nc	g
<i>Sertularella crassicaulis</i> (Heller, 1868)	E	g
<i>Sertularella cubica</i> Garcia, Aguirre & Gonzalez, 1980	E	g
<i>Sertularella cylindritheca</i> (Allman, 1888)	TA	g
<i>Sertularella fusiformis</i> (Hincks, 1861)	TA	g
<i>Sertularella gaudichaudi</i> (Lamouroux, 1824)	TA	g
<i>Sertularella gayi</i> (Lamouroux, 1821)	B	g
<i>Sertularella picta</i> (Meyen, 1834)	TA	g
<i>Sertularella polyzonias</i> (L., 1758)	C	g
<i>Sertularella robusta</i> Coughtrey, 1876	IP	g
<i>Sertularella simplex</i> (Hutton, 1872)	CT	g
<i>Sertularella tenella</i> (Alder, 1856)	C	g
<i>Sertularia distans</i> Lamouroux, 1816	CT	g
<i>Sertularia perpuzilla</i> Stechow, 1919	E	g
<i>Sertularia marginata</i> (Kirchenpauer, 1864)	CT	g
<i>Sertularia turbinata</i> (Lamouroux, 1816)	CT	g
<i>Thyroscyphus fruticosus</i> (Esper, 1793)	IP	g

Syntheciidae 1: 1 g

<i>Synthecium evansi</i> (Ellis & Solander, 1786)	MA	g
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Suborder **Proboscoida**

Superfamily Campanulariidae

Campanulariidae 24: 13 m, 10 g, 1 mg

<i>Campanularia hincksi</i> Alder, 1856	C	g
<i>Campanularia volubilis</i> (L., 1758)	B	g
<i>Clytia discoidea</i> (Mayer, 1900)	TA	m?
<i>Clytia gracilis</i> (Sars, 1851)	B	m?
<i>Clytia hemisphaerica</i> (L., 1767)	C	m
<i>Clytia linearis</i> (Thornely, 1899)	CT	m?
<i>Clytia mcCradyi</i> (Brooks, 1888)	CT	m?
(* <i>Clytia macrogonia</i> Bouillon, 1984)	IP	m?
<i>Clytia notiformis</i> (McCrady, 1859)	TA	m?
<i>Clytia paulensis</i> (Vanhoffen, 1910)	C	m?
<i>Clytia pentata</i> (Mayer, 1900)	CT	m?
<i>Clytia serrulata</i> (Bale, 1888)	IP	m?
<i>Gonothyræa loventi</i> (Allman, 1859)	C	g
<i>Hartlaubella gelatinosa</i> (Pallas, 1776)	B	g
<i>Laomedea angulata</i> Hincks, 1861	TA	g
<i>Lomedea calceolifera</i> (Hincks, 1871)	TA	g

<i>Laomedea flexuosa</i> Alder, 1856	TA	g
<i>Laomedea neglecta</i> Alder, 1856	B	g
<i>Obelia bidentata</i> Clarke, 1875	CT	m?
<i>Obelia dichotoma</i> (L., 1758)	C	m?
(*) <i>Obelia fimbriata</i> (Dalyell, 1848)	C	m?
<i>Obelia geniculata</i> (L., 1758)	C	m?
<i>Obelia longissima</i> (Pallas, 1766)	C	m?
<i>Orthopyxis asymmetrica</i> (Stechow, 1919)	E	g
<i>Orthopyxis crenata</i> (Hartlaub, 1901)	CT	g
<i>Orthopyxis integra</i> (Macgillivray, 1842)	C	mg

Order LAINGIOMEDUSAE 1: 1 m

Laingiidae 1: 1 m

<i>Kantiella enigmatica</i> Bouillon, 1978	IP	m
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Order LIMNOMEDUSAE 9: 7 m, 1 mg, 1 g

Armohydridae 1: 1 mg

<i>Armohydra janowiczi</i> Swedmark & Teissier, 1958	nc	mg
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Microhydrulidae 1: 1 g

<i>Microhydrula pontica</i> Valkanov, 1965	B	g
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Olindiasidae 6: 6 m

<i>Craspedacusta sowerbyi</i> Lankester, 1880	C	m
<i>Gonionemus vertens</i> A. Agassiz, 1862	CT	m
<i>Gossea corynetes</i> (Gosse, 1853)	MA	m
<i>Maeotias inexpectata</i> Ostroumoff, 1896	TA	m
<i>Olindias phosphorica</i> (Delle Chiaje, 1841)	TA	m
<i>Scolionema suvaense</i> (Agassiz & Mayer, 1899)	IP	m

Proboscidactylidae 1: 1 m

<i>Proboscidactyla ornata</i> (McCrary, 1857)	CT	m
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Order NARCOMEDUSAE 20: 20 m

Aeginidae 2: 2 m

<i>Aegina citrea</i> Eschscholtz, 1829	C	m
<i>Solmundella bitentaculata</i> (Quoy & Gaimard, 1833)	CT	m

Cuninidae 9: 9 m

<i>Cunina frugifera</i> Kramp, 1948	C	m
<i>Cunina globosa</i> Eschscholtz, 1829	CT	m
<i>Cunina lativentris</i> Gegenbaur, 1856 (doubtful, probably <i>C. globosa</i>)	CT	m
<i>Cunina octonaria</i> McCrary, 1857	CT	m
<i>Cunina polygona</i> (Haeckel, 1879) (doubtful)	E	m
<i>Cunina proboscidea</i> E. & L. Metschnikoff, 1871	E	m
<i>Cunina vitrea</i> Gegenbaur, 1856 (doubtful, probably <i>C. proboscidea</i>)	E	m
<i>Solmissus albescens</i> (Gegenbaur, 1856)	IP	m
<i>Solmissus incisa</i> (Fewkes, 1886)	CT	m

Solmarisidae 9: 9 m

<i>Pegantha mollicina</i> (Forsk., 1775) (doubtful)	E	m
<i>Pegantha rubiginosa</i> (Koelliker, 1853)	MA	m
<i>Pegantha triloba</i> Haeckel, 1879	CT	m
<i>Pegantha zonaria</i> (Haeckel, 1879) (doubtful)	E	m
<i>Solmaris corona</i> (Keferstein & Ehlers, 1861)	CT	m
<i>Solmaris flavescens</i> (Koelliker, 1853)	IP	m
<i>Solmaris leucostyla</i> (Will, 1844)	E	m
<i>Solmaris solmaris</i> (Gegenbaur, 1856)	E	m
<i>Solmaris vanhoeffeni</i> Neppi & Stiasny, 1911	E	m

Order TRACHYMEDUSAE 17: 17 m

Geryoniidae 2: 2 m

<i>Geryonia proboscidalis</i> (Forsk., 1775)	CT	m
<i>Liriope tetraphylla</i> (Chamisso & Eysenhardt, 1821)	CT	m

	Halicreatidae 1: 1 m		
<i>Haliscera conica</i> Vanhoffen, 1902		CT	m
(*) <i>Halitrephes maasi</i> Bigelow, 1909		CT	m
	Pctasidae 1: 1 m		
<i>Petasis atavus</i> Haeckel, 1879		MA	m
	Ptychogastridae 1: 1 m		
<i>Ptychogastria asteroides</i> (Haeckel, 1879)		E	m
	Rhopalonematidae 12: 12 m		
<i>Aglaura hemistoma</i> Péron & Lesueur, 1810		CT	m
<i>Amphogona pusilla</i> Hartlaub, 1909		IP	m
<i>Arctapodema ampla</i> (Vanhoffen, 1902)		CT	m
<i>Homæonema platygonon</i> Browne, 1903		TA	m
<i>Panthachogon haeckeli</i> Maas, 1893		C	m
<i>Panthachogon militare</i> (Maas, 1893)		TA	m
<i>Persa incolorata</i> McCrady, 1857		CT	m
<i>Ransonia krampi</i> (Ranson, 1932)		TA	m
<i>Rhopalonema funerarium</i> Vanhoffen, 1902		CT	m
<i>Rhopalonema velatum</i> Gegenbaur, 1856		CT	m
<i>Sminthea eurygastra</i> Gegenbaur, 1856		CT	m
<i>Tetrorchis erythrogaster</i> Bigelow, 1909		CT	m
	Order ACTINULIDAE 3: 3 g		
	Halammohydridae 2: 2 g		
<i>Halammohydra octopodides</i> Remane, 1927		C	g
<i>Halammohydra shulzei</i> Remane, 1927		C	g
	Otohydridae 1: 1 g		
<i>Otohydra vagans</i> Swedmark & Teissier, 1958		MA	g