# Origin and biogeography of the deep-water Mediterranean Hydromedusae including the description of two new species collected in submarine canyons of Northwestern Mediterranean*

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SUMMARY: Two new species of hydromedusae (*Foersteria antoniae* and *Cunina simplex*) are described from plankton collected in sediment traps placed in the Lacaze-Duthiers Submarine Canyon and along Banyuls-sur-Mer coast (northwestern Mediterranean). The Mediterranean hydromedusan deep-water fauna contains 41 species which represent 45.5 % of the world-wide deep-sea hydromedusae fauna (90) and 20% of the total number of Mediterranean hydromedusae (204). The Mediterranean deep-water hydromedusan fauna is characterised by a large percentage of holoplanktonic species (61%), mainly Trachymedusae. Nevertheless, contrary to the general opinion, the percentage of meroplanktonic species is equally high. The most original features of this fauna lies however in the importance of the number of endemic species (22%) and in the fact that the majority of them are meroplanktonic Leptomedusae with a supposed bathybenthonic stage. Some of the endemic species could still represent relics of the primitive Tethys fauna having survived to the Messinian crisis. The origin of the Mediterranean deep-water hydromedusan fauna is discussed and a general hypothesis is proposed.

*Key words*: Hydromedusae, submarine canyons, western Mediterranean, sediment traps, deep-sea fauna, biodiversity, *Solmissus*, Rhopalonematidae new diagnosis, *Foersteria antoniae*, *Cunina simplex*.

RESUMEN: HIDROMEDUSAS PROFUNDAS DEL MEDITERRÁNEO: UN ESTUDIO QUE INCLUYE LA DESCRIPCIÓN DE DOS NUEVAS ESPECIES RECOLECTADAS EN CAÑONES SUBMARINOS DEL MEDITERRÁNEO OCCIDENTAL.– Se describen dos especies nuevas a partir de ejemplares recolectados mediante trampas de sedimento del cañón submarino de Lacaze-Duthiers situado en frente de la costa de Banyuls-sur-Mer (Mediterráneo noroccidental). La fauna profunda de hidromedusas en el Mediterráneo contiene 41 especies que representan 45.5 % de la fauna mundial del grupo y el 20% de la fauna de hidromedusas del Mediterráneo. La fauna Mediterránea de hidromedusas profundas se caracteriza por un gran porcentaje de especies holoplanctónicas (61%), fundamentalmente Trachymedusas, sin embargo, contrario a la opinión generalizada, el porcentaje de especies meroplanctónicas es igualmente importante (39%). La característica más interesante de esta fauna es el número de especies endémicas (22%) y el hecho de que la mayoría de estas especies son meroplanctónicas (Leptomedusas) con una supuesta fase bentónica. Algunas de estas especies endémicas, podrían ser especies relictas (endémica insular) de la fauna primitiva del Tetis que sobrevivieron a la crisis Mesiniana. Se discute el origen de la fauna de hidromedusas profundas en el Mediterráneo y se presenta una nueva hipótesis.

*Palabras clave*: Hydromedusae, cañones submarinos, Mediterraneo occidental, trampas de sedimento, fauna profunda, biodiversidad Mediterránea, *Solmissus*, diagnosis nueva Rhopalonematidae, *Foersteria antoniae*, *Cunina simplex*.

## INTRODUCTION

In spite of the fact that the general plankton biomass diminishes exponentially with depth, numerous observations show that a local increase in biomass and diversity occurs near the pelagic-benthos boundary (Grice and Hulsemann, 1965, 1967; Vinogradov, 1968; Wishner, 1980; Fashman, 1984; Larson *et al.*, 1992) and for instance the diversity of the hydromedusan fauna augments between 500 and 800 m (Kramp, 1968). Hydromedusae are among the main predators of the ocean and constitute a significant but often underestimated constituent of the pelagic deep fauna. Data about their composition, distribution, trophic relations and relationships with other oceanic strata are very scarce, based on limited observations. They seem to play a much more important role in oceanic transfer of energy than previously thought.

The knowledge of the deep-sea Hydroidomedusae fauna is still incomplete and biased even for the polyp stage, for which the sampling processes do not introduce great depth uncertainties; in fact only the species with hard skeletons (Leptomedusae polyps) are collected in good conditions by dredging. There is therefore an unnatural balance in favour of the thecate hydroids, three times more thecate deep-waters polyps than athecate ones have been described (see for instance Vervoort, 1966; Goy, 1995). The depth and vertical distribution of hydromedusae is often uncertain owing to the sampling methodology, generally only the upper limit of their vertical distribution is known and it is practically impossible from literature to distinguish between meso- and bathypelagic species. Furthermore, the sampling with plankton nets, even at discrete depths, damage or break up most of the delicate species which then cannot be properly identified.

Most deep-sea hydromedusae are known from mid-water and very few have been reported inhabiting the near bottom water layers. However, in recent years direct observations from submersibles have shown that deep-sea medusae can be abundant near the sea floor (Mills,1982; Mackie 1985; Larson *et al.*, 1992).

Under the auspices of the EUROMARGE NB Project, several moorings equipped with sediment traps were placed inside and around several submarine canyons in the North West Mediterranean. The main objective of this project was to study particle flux transferred from the continental shelf to the continental slope through the submarine canyons (Puig and Palanques, 1995). An important set of gelatinous zooplankton was collected from the traps in addition to the sediment particles. Gelatinous specimens were the most abundant group of macro-organisms in the samples. Their collection allowed Gili *et al.* (in press) to describe several new deep-sea hydromedusae and to postulate the presence of a very unusual planktonic community in the canyons which is probably supported by the flux and storage of organic material coming from the continental shelf. The specific composition and abundance of the medusae populations seems different between various canyons. The techniques of sediment trap sampling and of direct observation and collection by submersibles both avoid most of the inconveniences cited above for plankton sampling.

The objective of the present contribution is to analyse the relationship between ecology and biodiversity of the bottom deep-water Mediterranean hydromedusan community and its relationships with the deep-water fauna of other seas. The deep-water hydromedusan fauna of some submarine canyons is described including two new species. Some hypothesis concerning the origin and dispersion of the Mediterranean deep-sea medusae are explored.

## MATERIALS AND METHODS

Mooring lines supporting a total of four PPS3 sediment traps were placed in several canyons of the northwestern Mediterranean sea. Three lines were deployed nearby both the Lacaze-Duthiers (Banyuls) and Planier (Marseille) canyons (Fig. 1). The same deployment strategy was used within each of the canyons: two mooring lines were located inside the canyon at 500 m and 1000 m water depths respectively. Both moorings had a sediment trap 30 m above the bottom and the mooring at 1000 m also supported a second trap located in mid-water 500 m above the bottom. The third mooring line was deployed in the interflow at 1000 m depth, with a sediment trap 30 m above the bottom. In the North Balearic slope -which is not a real canyon- two moorings were deployed, one at 500 m depth with a sediment trap 300 m above the bottom and another at 1000 m depth with two traps at 30 and 500 m above the bottom. The moorings were deployed from May 1994 to May 1995 in the Balearic slope and from October 1993 to December 1995 in the Lacaze-Duthier and Planier canyons. Each sediment trap had 12 rotary collectors that were sampled every 15 or 16 days, depending on the month.
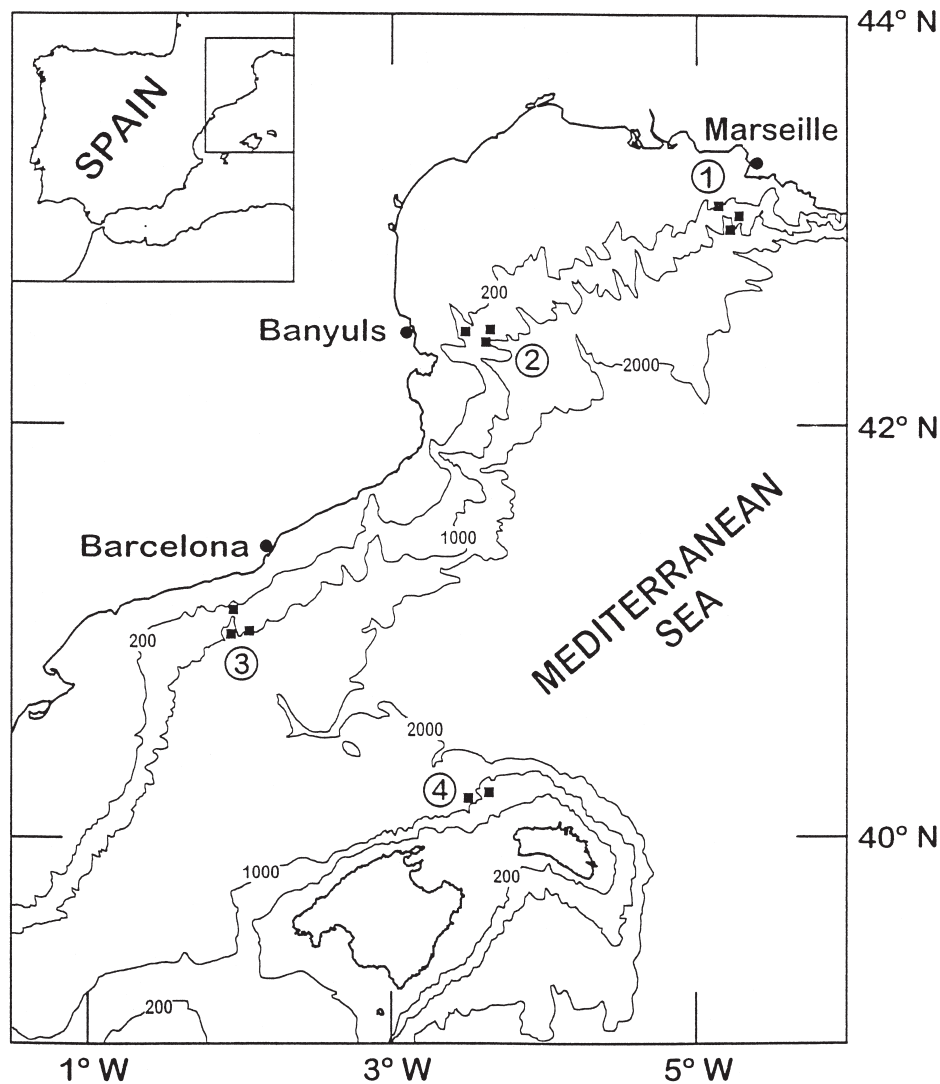
FIG. 1. – General map of the study area indicating the areas where the sediment traps were located.

The collected particle samples were processed in the laboratory. Each collector has a maximum sample volume of 100 ml. The total samples were divided into several aliquots and the biological components not forming part of the vertical flux of matter ("swimmers") were removed and studied separately. The sediment traps collected numerous swimmers that entered the sample containers and died because of the presence of formaldehyde. Gelatinous species were preserved in excellent condition and were immediately separated from the rest of the samples in order to carry out taxonomic studies. Data for swimmers are not quantitative but all organisms were counted in order to get a general pattern of species distribution and abundance among the different locations where the traps were located.

RESULTS

**List of the species collected**

(The species marked with an asterisk are discussed in the text)

ANTHOMEDUSAE
**Filifera**
Calycopsidae
   *Calycopsis simplex* Kramp and Damas, 1925*
Pandeidae
   *Amphinema rubra* (Kramp, 1957)*
**Capitata**
Euphysidae
   *Euphysa aurata* Forbes, 1848

Zancleidae
*Zanclea* spp.

LEPTOMEDUSAE
**Conica**
Mitrocomidae
*Foersteria antoniae* n. sp.
Tiarannidae
*Modeeria rotunda* (Quoy and Gaimard,1827)

NARCOMEDUSAE
Cuninidae
*Cunina globosa* Eschscholtz, 1829*
*Cunina simplex* n.sp.
*Solmissus albescens* (Gegenbaur, 1857)*
Solmarisidae
*Solmaris flavescens* (Kölliker, 1853)

TRACHYMEDUSAE
Halicreatidae
*Haliscera bigelowi* Kramp,1947*
*Haliscera racovitzae* (Maas,1906)*

Ptychogastriidae
*Ptychogastria asteroides* (Haeckel, 1879)
Rhopalonematidae
*Arctapodema australis* (Vanhöffen, 1902)*
*Homoeonema platygonon* Browne, 1903*
*Persa incolorata* McCrady, 1859
*Sminthea eurygaster* Gegenbaur, 1857

**Species descriptions**

ANTHOMEDUSAE
Family Calycopsidae
***Calycopsis simplex*** Kramp and Damas, 1925
(Fig.2)

Material: Lacaze-Duthier canyon, 500m depth, December 1994, 1 specimen.

This species was orignally described from Norwegian waters. Goy (1972) found one specimen in the Mediterranean (Villefranche-sur-Mer), this is the second record from Mediterranean waters. It is uncommon worldwide.
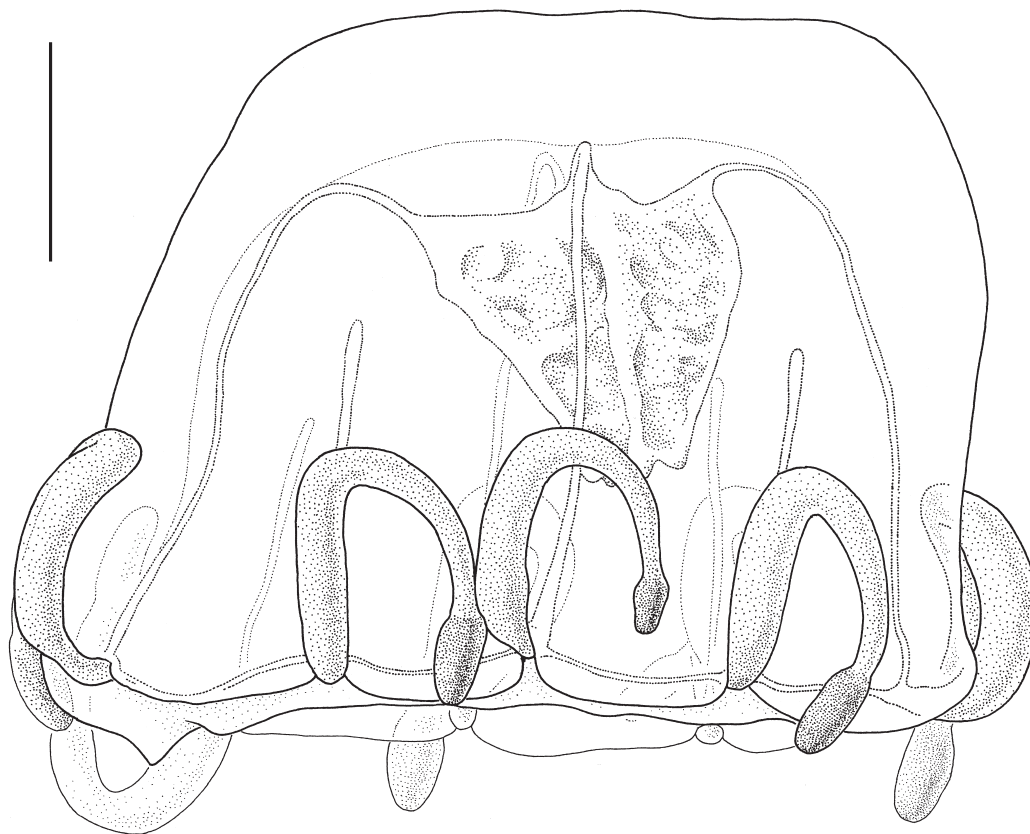


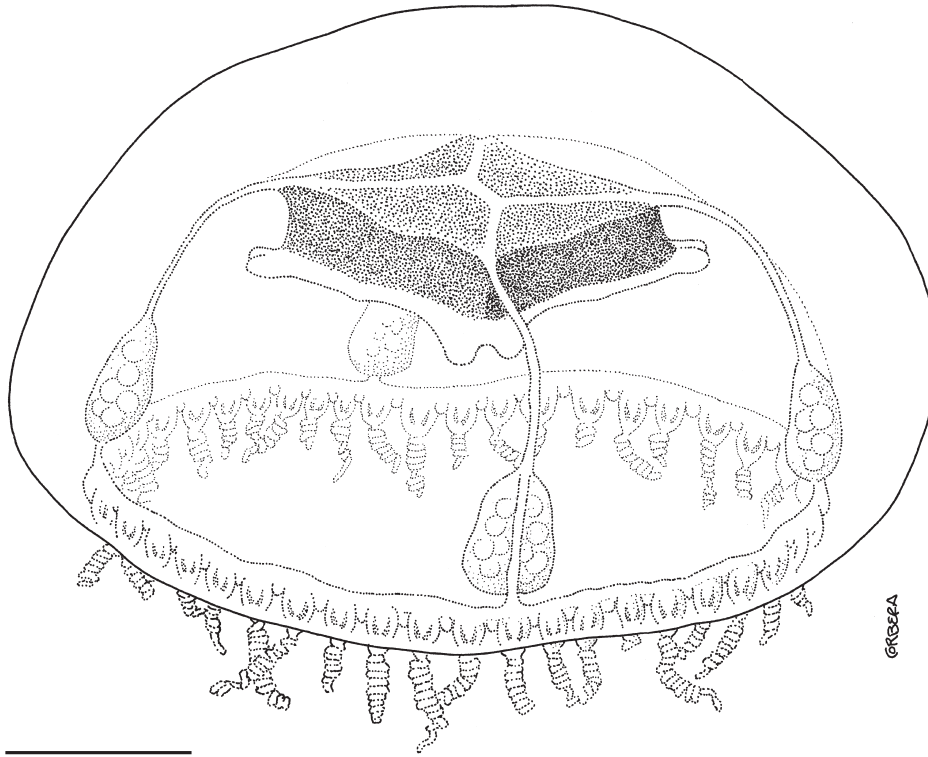FIG. 2. – *Calycopsis simplex*, lateral view. Scale bar = 3 mm.

Fig. 3. – *Foersteria antoniae*, general view. Scale bar = 1 mm

Family Pandeidae
***Amphinema rubra*** (Kramp, 1957).

Material: Balearic slope, 700m depth, January 1995,1 specimen.

This species was described from the Antarctic waters (South Orkney Islands). Goy (1972) found 1 specimen in the Mediterranean (Villefranche-sur-Mer) between 600 and 300 m depth. This is the second record from Mediterranean waters.

LEPTOMEDUSAE
Family Mitrocomidae
***Foersteria antoniae*** n. sp.
(Fig. 3 and 4)

Material: Lacaze-Duthiers canyon, 1000 m depth, April 1994, 2 specimens; 1000 m depth, May 1994, 3 specimens; Planier canyon, 500 m depth, May 1994, 1 specimen.

Holotype deposited at the Institut de Ciències del Mar (ICM-CSIC) (Barcelona) Cnidarian Collection, Reg. LEP 0017-1. Five paratypes, also deposited in the ICM collections, labelled LEP 0017-2. Holotype collected at the Lacaze-Duthiers canyon ( 40° 26' N, 3° 33' E), 1-15 April 1994 at 500 m above the bottom over the 1000 m isobath.

Etymology: This new species is dedicated to Ms. Antonia Cruz, suddenly deceased in August 1996, in honour of her enthusiastic and valuable work in plankton research and for her extraordinary kindness and warm friendship.

Diagnosis: Umbrella flatter than a hemisphere, 6 mm wide, 3 mm high; 40 marginal tentacles; manubrium very short, very broad, 1/3 of umbrella, with quadratic base, colour dark purple-brown; mouth with 4 simple, not groove-shaped lips; marginal bulbs large, rounded without cnidocyst deposits; gonads spherical to elongate depending on sex, on the distal half of radial canals; 40 open statocysts.

Description: Umbrella flatter than a hemisphere, almost quadratic from above, up to 6 mm wide and 3 mm high; jelly rather thick; without peduncle; up to 40 long, hollow, marginal tentacles evenly covered with cnidocysts; marginal tentacular bulbs large, rounded, without cnidocyst deposits, each with two lateral masses of brown pigmented granules; without marginal or lateral cirri; manubrium very short and large, with broad quadratic base, 1/3 of the width of the umbrella, intensely and uniformly coloured in dark purple-brown except along the way of the radial canals which are transparent; mouth with 4 simple, very short lips, not groove-shaped, bright white in
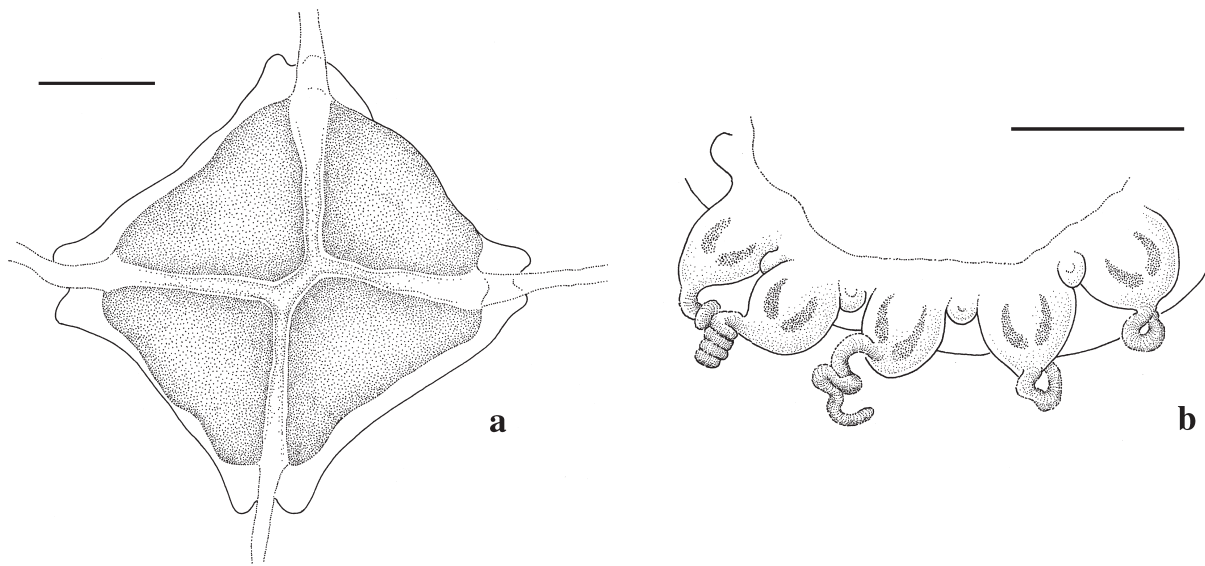
FIG. 4. – *Foersteria antoniae*; a, aboral view of the stomach (scale bar = 0.5 mm) and b, detail of the umbrella margin (scale bar = 0.5 mm).

TABLE 1. – Comparison between the different species of the genus *Foersteria* .

|  | *F. purpurea* | *F. bruuni* | *F. araiae* | *F. antoniae* n.sp. |
|---|---|---|---|---|
| Umbrella | hemispherical up 30mm wide | flat, quadratic 5.5 -15mm wide 1/2 as high as wide | hemispherical 7 mm wide | flatter than hemispherical 6mm wide, 3mm high, quadratic |
| Peduncle | short | none | none | none |
| Tentacles | up to 120 | 40-70 | up to 40 | up to 40 |
| Tentacle bulbs | small, conical, without cnidocysts | swollen, large with cnidocyst deposits | conical without cnidocyst deposits | large, rounded, without cnidocyst deposits |
| Radial canal | narrow light purple | narrow | narrow | narrow |
| Manubrium | rather small, color purple | average size 1/5 the width of umbrella, 1/2 high of umbrella | very short, small, square, 1/7 width and height umbrella, color light brown, with 4 interradial dark brown lines | very short and broad, 1/3 umbrella width, intensely and uniformly dark purple-brown, except in the perradii |
| Lips | 4 elongated, highly folded lips, color purple | 4 long, slightly undulated lips | 4 short, simple, groove-shaped, bright white lips | 4 short, simple, not groove-shaped, bright white lips |
| Gonads | curtain like, split longitudinally, almost entire length of radial canals | oval, laterally flattened, on distal half of radial canals | oval or rounded, rather small, near circular canal | oval in female, with very few eggs (5-15), bigger and elongate in male, both near circular canal |
| Sense organs | more than 40 | 1 vesicle between 2 succesive tentacles, (40 - 70) | 2 (1-3) between 2 succesive tentacles (80) | 1 between succesive tentacles (40) |
| Distribution | British Columbia, Monterrey bay | Bay of Bengal, Indian Ocean | Barcelona, Mediterranean Sea | Banyuls-sur-Mer, Mediterranean Sea |
| Depth | more than 350 m | 125-250 m | 600-1200 m | 500 m |

colour; mouth rim with cnidocysts; with 4 simple narrow radial canals; female gonads spherical, rather small, near the circular canal, each with very few (5-15) big eggs, male gonads larger, about the 4/5 of the distal half of the radial canal, in both sexes the distal end of the radial canals remains free; 1 (rarely 2) open marginal statocysts between successive tentacles (up to 40); without ocelli.

Discussion: The present material is ascribed to the genus *Foersteria,* which is defined as Mitrocomidae with four radial canals, with numerous open marginal statocysts, without ocelli and without marginal cirri. Three species are presently recognised in this genus, *F. purpurea* (Foerster, 1923), *F. bruuni* (Navas, 1969) and *F. araiae* Gili *et al.* (in press) their characteristics are summarised in Table 1. *Foersteria antoniae* is close to *F. araiae* from which its differs nevertheless by its flatter umbrella, by the shape of the marginal bulbs, the intense and characteristic dark purple-brown colour of its particularly broad manubrium, lytle absence of groove-like lips, by the small number of eggs present in the female gonads and the relatively large size of male gonad.

# NARCOMEDUSAE
## Family Cuninidae
### *Cunina globosa* Eschscholtz, 1829
(Fig. 5 and 6)

Material: Balearic slope, 700 m depth, April 1994, 1 specimen.

This species is known from the Atlantic and Indo-Pacific and has been described from the epipelagic waters of the western Mediterranean (Gili *et al.*, 1987; Medel *et al.*, 1996). Our single deep-water specimen is in very good shape and corresponds in all respects with the description of the species. Mayer (1910) stated that *Aegineta globosa* Gegenbaur,1857 of the Mediterranean could possibly be identical with *Cunina globosa* from the Pacific.
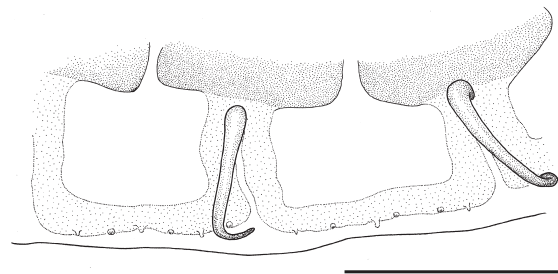
FIG. 5. – *Cunina globosa*, detail of the umbrella margin (scale bar = 2 mm).
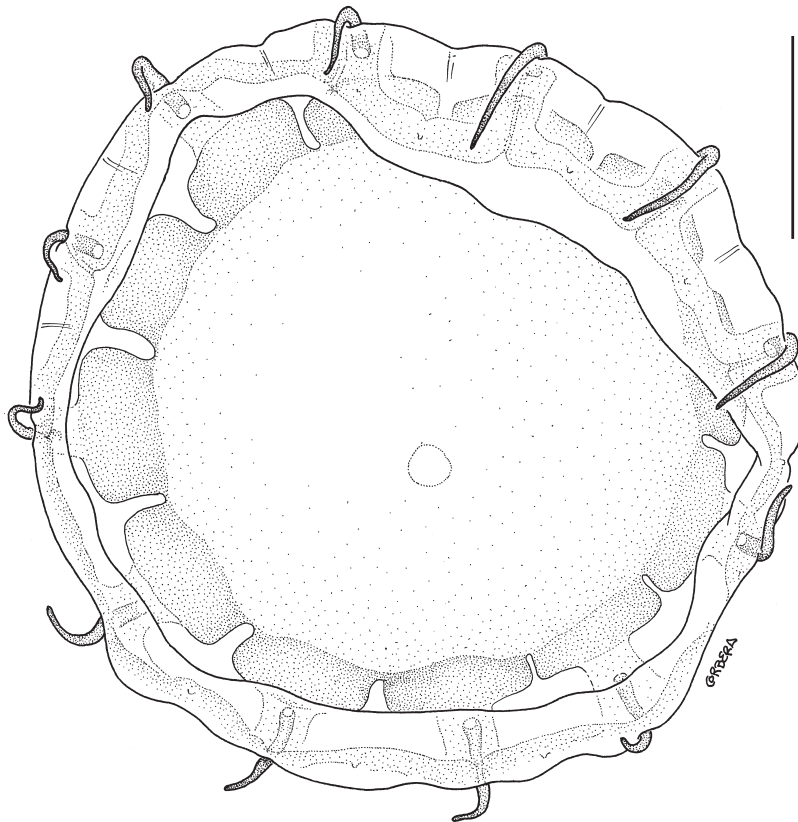
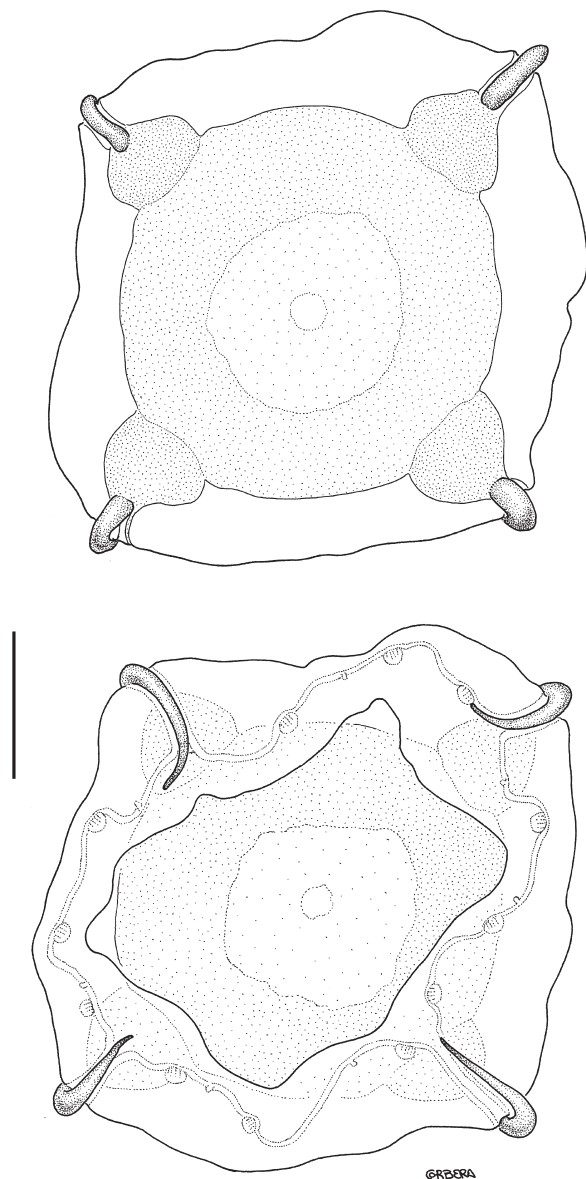FIG. 6. – *Cunina globosa*, oral view (scale bar = 5 mm).

FIG. 7. – *Cunina simplex*; a, aboral view and b, oral view (scale bar = 1 mm).

## *Cunina simplex* n. sp.
### (Fig. 7)

Type material: Holotype deposited in the Institut de Cièncès del Mar (ICM-CSIC) (Barcelona) Cnidarian collection, Reg. NAR 0017-1. One paratype, also deposited in the ICM collection, labelled NAR 0017-2. Holotype collected at the Lacaze-Duthiers canyon ( 40° 26' N, 3° 33' E) 1-15 April at 500 m above bottom over the 1000 m isobath.

Etymology: The species name *simplex* was chosen because of the simplicity of its structure.

Diagnosis: *Cunina* with 4 manubrial pouches and 4 primary tentacles.

Description: Umbrella higher than a hemisphere almost globular, 3.7 mm wide and 2.8 mm high; mesoglea thick, manubrium large, circular with 4 small, perradial, tongue-shaped, undivided manubrial pouches narrowing in width from base outwards; septa between pouches very wide; with 4 primary tentacles leaving umbrella opposite to the centre of each stomach pouch; with 4 peronia; without secondary tentacles on umbrella margin; gonads on manubrium and walls of the manubrial pouches; with a narrow peripheral canal system; marginal lappets rectangular, large; with 3 small, circular otoporpae and 1-2 statocysts per quadrant.

Discussion: This species is refered to the family Cuninidae, genus *Cunina* Mc Crady, 1859 by the presence of perradial manubrial pouches, of a peripheral canal system and otoporpae. It is the only mature *Cunina* known with only 4 primary tentacles and 4 manubrial pouches and is therefore here considered as a new species.

## *Solmissus albescens* (Gegenbaur, 1857).

Material: *Solmissus albescens* (Gengenbaur, 1857): Institut Royal des Sciences Naturelles de Belgique, I.G. 27.838: Ville-franche-sur-Mer, France, 1955, 1 specimen; Naples, Italy, 06/06/1963, 1 specimen.

Lacaze-Duthiers canyon: 1000 m depth, July 1994, 2 specimens; December 1994, 4 specimens, January 1995, 2 specimens; Planier canyon: 500 m depth, January 1995, 2 specimens; 500 m depth, February 1995, 1 specimen; 1000 m depth, December 1994, 4 specimens; 1000 m depth, January 1995, 1 specimen; 1000 m depth, February 1995, 2 specimens; 1000 m depth, November 1995, 1 specimen; 1000 m depth, July 1995, 1 specimen; 1000 m depth, August 1995, 1 specimen. Balearic slope: 700 m depth, May 1994, 3 specimens; July 1994, 2 specimens; August 1994, 1 specimen; October 1994, 1 specimen; December 1994, 2 specimens; February 1995, 2 specimens.

*Solmissus marshalli* Agassiz and Mayer, 1902. Institut Royal des Sciences Naturelles de Belgique, I.G. 27.838: Papua New Guinea, 1 specimen.

Discussion: Medusae of the genus *Solmissus* are among the most common in our collections. This genus is characterised by the presence of undivided perradial manubrial pouches, the absence of a peripheral canal system and otoporpae. The genus *Solmissus* presently comprises six species: *S. albescens*, *S. incisa* and *S. marshalli* are generally accepted as well defined species, *Solmisssus faberi* and *Solmissus bleekii* are considered by Kramp (1961) as doubtful, *S. atlantica* Zamponi, 1983 is also doubtful, being insufficiently described and illustrated and probably belonging to another genus.

The members of the genus *Solmissus* are closely allied and the characters used for specific identifica-

TABLE 2. – The table below summarizes the diagnostic differences generally accepted between the different species of *Solmissus*.

| | *S. albescens* | *S. incisa* | *S. marshalli* |
|---|---|---|---|
| Umbrella size (mm) | up to 50 | up to 100 | up to 62 |
| Umbrella surface | umbrella scattered with small gelatinous warts and cnidocysts patches | smooth | smooth |
| Number of tentacles, lappets and manubrial pouches | maximum 16 | 20-40 | 8-20, usually16 |
| Shape of manubrial pouches | pentagonal | oval, longer than wide | rectangular |
| Shape of marginal lappets | rectangular with rounded outer margin | rectangular | square |
| Number of statocysts per lappet | 5-8 | 2-5 | 15- 21 |
| Distribution | Mediterranean Sea | Atlantic, Indian and Pacific Oceans | Atlantic, Indian and Pacific Oceans |

tion are known to be subject to individual variation so that, for instance, *S. incisa* has sometimes been considered to represent only a giant form of *S. albescens* (Ranson, 1936; Russell, 1953). Bigelow (1909) states that *S. marshalli* is so close to *S. albescens* that they could merely represent geographical races. More recently Mills *et al*. (1996) underlined the difficulty in distinguishing between *S. albescens* and *S. marshalli,* acknowledging that *S. marshalli* may be a junior synonym of *S. albescens* and remarked that even specialists have difficulties in assigning species name *S. marshalli* or *S. incisa* to some specimens.

From Table 2 it may be concluded that *S. albescens* is distinct from the other species by its smaller size, by its exumbrellar ornamentation, by the pentagonal shape of its manubrial pouches and its endemicity. *S. incisa* not only attains a much bigger maximum size than *S. albescens* but present also a greater number of tentacles, manubrial pouches and marginal lappets. From Kramp (1959, 1965, 1968) and the above mentioned literature it appears that the specimens of *S. incisa* falling in the size range of *S. albescens* always have more than 16 marginal tentacles, which is the maximum number recorded for the latter species, and that the manubrial pouches of *S. incisa* are oval, elongated instead of pentagonal, on the other hand their number of statocysts falls almost in the same range as those of *S. albescens*.

*Solmissus marshalli* also reaches a much larger maximum size than *S. albescens*, its number of ten-

tacles is generally 16 as in *S. albescens*, but can attain 20 and the number of statocysts is much greater 15-21 instead of 5-8, the manubrial pouches are rectangular instead of pentagonal and their marginal lappets are square instead of rectangular. The main difference between *S. marshalli* and *S. incisa* lies in the number of statocysts, much greater in *S. marshalli*, and in the shape of their manubrial pouches and marginal lappets (see Table 2). Theoretically the three species seem thus rather easy to identify at any given size, but practically this is generally not at all easy, due to the individual variations of some of the above mentioned characters and to the fragility of the specimens which are often in bad condition of preservation Our specimens show a size ranging from 10 to 35 mm in diameter, all have 16 primary tentacles (1 specimen has 20), 16 perradial manubrial pouches and marginal lappets; when still present, the manubrial pouches are pentagonal in shape; the marginal lappets are rectangular with a rounded outer margin. By these characters our specimens show clear affinities with *S. albescens,* but they present only a maximum of 6 statocysts (generally 4) instead of 5-8 per marginal lappet and mainly lack the small exumbrellar gelatinous warts considered to be characteristic of this species. The central part of the umbrella is completely smooth, the under-tentacular exumbrellar portion has a more irregular surface presenting cnidocyst patches similar to those described in *S. albescens* and numerous scattered structures formed by refringent vesicules disposed in round or

oval crateriform rings. Mills *et al.* (1996) found numerous *Solmissus* in the Alborán Sea apparently closely related to *S. albescens* but also without exumbrellar warts, some with cnidocyst patches extending above the lappets onto the bell.They finally considered them to be *S. albescens.* based primarly on geographical location. Specimens decribed as *Solmissus albescens* from Villefranche-sur-Mer, France and Naples, Italy also did not show the distinctive gelatinous warts, but their lappets were covered with cnidocyst patches similar to those observed in our specimens and illustrated by Mills and Goy (1988, Fig. 4b). *Solmissus marshalli* from Papua New Guinea on the contrary did not show such structures. Our specimens are finally assigned to *S. albescens* whose description must be slightly modified as follows:

*Solmissus albescens* (Gegenbaur, 1857): (mainly after Mayer, 1910; Trégouboff and Rose, 1957; Kramp, 1959, 1961): Umbrella up to 50 mm in diameter; central part of umbrella doubly convex, lenticular; bell collar thin, flexible, contractile. Exumbrella scattered either with small but distinct gelatinous warts and/or with flat discoid or elongated cnidocyst patches that may be localized only on the lappets. Velum broad. Manubrium large, circular, with wide mouth opening and with 14-16 marginal perradial pouches, pentagonal in shape and somewhat wider than long, their outer angles lying under the tentacle roots; 14 -16 tentacles nearly as long as the umbrella diameter, tapering and not very flexible; about 14-16 marginal lappets, rectangular but with rounded angles on their outer margin, each with 5-8 statocysts. Gonads developed in the subumbrellar ectoderm of manubrium and manubrial pouches. Medusae colourless except gonads and tentacles, which may be milky white

TRACHYMEDUSAE
Family Halicreatidae
*Haliscera bigelowi* Kramp,1947.

Material: Balearic slope, 700 m depth, January 1995, 1 specimen.

This species is known from bathypelagic waters of the Atlantic, the Indo-Pacific and the Southern oceans (Kramp 1947-1968; Thuesen & Childress, 1994). First record in the Mediterranean Sea.

*Haliscera racovitzae* (Maas,1906).

Material: Planier canyon, 1000 m depth, September 1994, 1 specimen.

This is the first record of the species from the Mediterranean. It is bathypelagic in the Atlantic, in the Indo-Pacific and in the Antarctic and Sub-Antarctic waters (Kramp, 1965-1968).

Family Rhopalonematidae
*Arctapodema australe* (Vanhöffen, 1902).

Material: Planier canyon, 500 m depth, April 1994, 1 specimen.

One specimen has been found, not in good shape, but very similar in most respect to *A. australe.* This species was known only from the Southern Ocean (Kramp 1957-1968) in intermediate and deepwaters, it is new for the Mediterranean. Mills *et al.,* (1996) collected two specimens of *Arctapodema,* which could not be clearly assigned to one of the presently described species, in the Alborán sea.

*Homoeonema platygonon* Browne, 1903.
(Figs. 8, 9 and 10)

Maas 1903, p. 15, pl.1 fig. 8; Browne, 1903, p.21, pl. 2 figs. 2, 3; ? Grobben, 1915, p. 4; ?Neppi, 1915, p. 4; ? Pell, 1918, p. 22, 28, fig. 3; ? Neppi, 1920, p. 91; Kramp and Damas, 1925, p. 318; Runnström, 1932, p. 30; Bernstein, 1934, p. 26, 53; ? Pell 1938, p. 927; Jaschnov,1939, p. 112; Kramp, 1947,p. 17, pl. 2, fig. 6; Vannucci, 1951, p. 112-117; Kramp, 1959, p.185, fig. 269; Kramp, 1961, p. 258.

Material: 1 specimen, Zoologisk Museum, Copenhagen; Herløfjord, Norway, 300 m; Kramp and Damas, Oct. 1908. Foix canyon (Barcelona), 1000 m depth, May 1993, 1 specimen; Lacaze-Duthiers canyon, 500 m depth, June 1994, 1 specimen, July 1994, 1 specimen; Planier canyon, 500 m depth, May 1994, 2 specimens, July 1994, 2 specimens, October 1994, 1 specimen, April 1995, 4 specimens, May 1995, 1 specimen, July 1995, 2 specimens; Balearic slope, 700 m depth, July 1994, 2 specimens, April 1995, 1 specimen, May 1995, 2 specimens.

Description: Umbrella bell-shaped, higher than wide, with round or more rarely conical apex, up to 2 mm high, mesoglea thin, no peduncle; no apical process. Up to 80 closely crowded marginal tentacles, 3/4 of umbrella length, issued from an exumbrellar marginal ring rich in cnidocysts and irregular inclusions; base of tentacles enlarged, containing cnidocysts and inclusions, giving rather abruptly rise to the proximal parts of the tentacles which are almost devoid of cnidocysts and have their endodermal core built by large cubical chordal cells (perhaps flexible), the distal parts of the tentacles are crowded with cnidocysts, and their endodermal core is formed by flattened, disk-shaped, chordal cells; no cirri or non tentacular bulbs. Eight fairly wide radial canals, full of irregular inclusions, circular canal not visible within the marginal cnidocyst ring. Velum very large. Manubrium short, flat, quadratic,
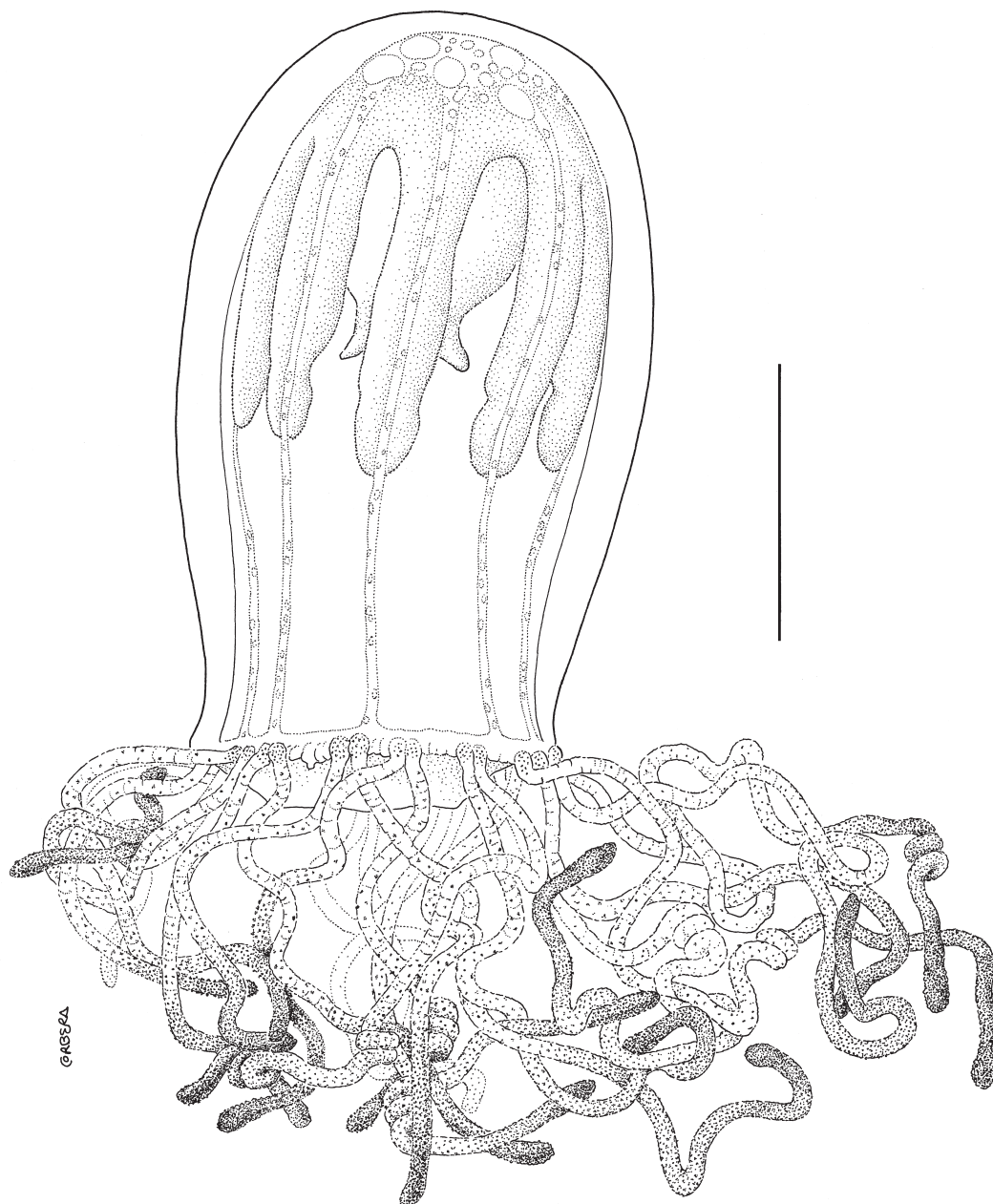
FIG. 8. – *Homoeonema platygonon*, lateral view of an adult specimen. Scale bar = 0.5 mm.

apical part containing numerous fat droplets and irregular inclusions (crystals); mouth with 4 simple, short, recurved lips, the tips armed with stenoteles. Gonads, in adults 8 elongated masses along the 1/2 or 2/3 of the proximal part of the radial canals, their most proximal sections being fused and forming a ring surrounding the base of the manubrium, in young specimens the gonads appear first as oval masses on the proximal third of the radial canals and then slowly extend downwards and upwards, they finally become confluent in the upper interradial parts and encircle the manubrial base. Cnidocysts:

apparently several types, one of which is stenoteles. Sense organs difficult to observe obscured by the numerous and dense tentacles, 3 or 4 pendant marginal sensory organs with numerous inclusions have been observed dispersed in some specimens.

Distribution: After Kramp (1947, 1959) several medusae belonging to different genera have been referred to the genus *Homoeonema*. *H. platygonon* appears to be quite common in the Norwegian fjords; in the Kara Sea; between Scotland, Iceland and Greenland; it has also been reported from the
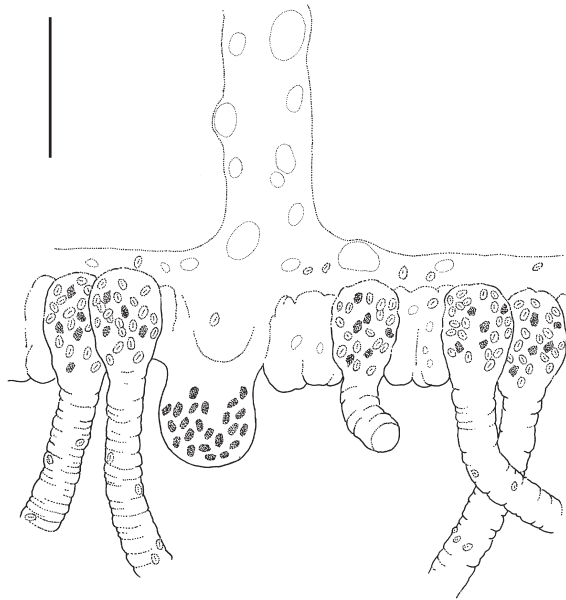
FIG. 9. – *Homoeonema platygonon*, detail of the umbrella margin (scale bar = 0.05 mm).

coast of Brazil; the Adriatic sea and Naples. The presence of *Homoeonema platygonon* in Brazilian waters and in Mediterranean was however considered as questionable by Kramp (1961). Recently, *Homoeonema* has been reported from the Mediterranean on bases of previous cited references by Boero *et al*. (1993) and by Benovic *et al*. (1996), the present report unquestionably confirms its presence in the Mediterranean.

Depth: outside Mediterranean canyons: 200 to 400 m in Bergen fjords, young specimens in shallower waters than adults; 10 to 155 m in Kara Sea; in the canyons of North West Mediterranean between 500 and 1000 m depth.

Discussion: The genus *Homoeonema* has been included in the Rhopalonematidae. The medusae of this family are characterised as follows: Trachymedusae with a narrow manubrium; with or without peduncle; without centripetal canals; with 8 (rarely more) narrow radial canals; with a mouth with lips; with gonads on radial canals, either globular, linear, or pendant; with marginal tentacles evenly distributed, sometimes of two types; each tentacle of uniform structure throughout; with free, rarely enclosed, marginal sensory clubs. In this family *Homoeonema* is distinguished mainly by the gonad position, forming a continuous band at the base of the manubrium and extending outwards along the 8 radial canals, whereas all the other gen-
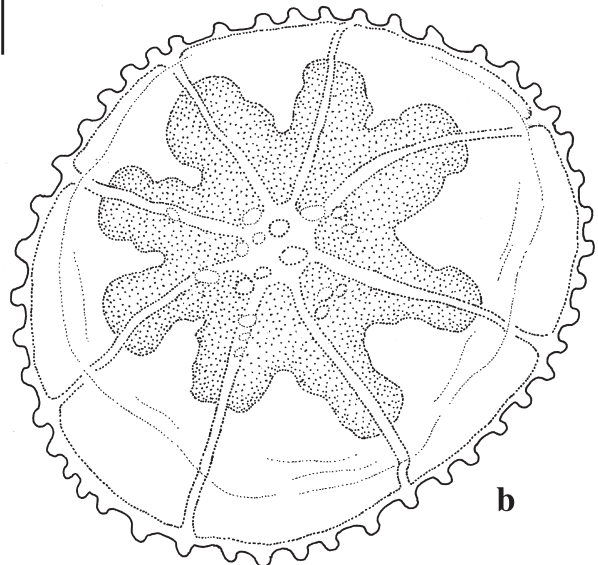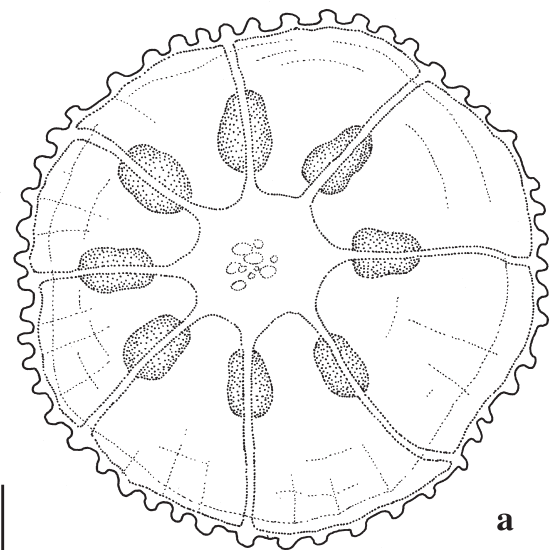


FIG. 10. – *Homoeonema platygonon*; a, aboral view of a juvenile specimen, and b, aboral view of an adult specimen (scale bar = 0.5 mm).

era of Rhopalonematidae have isolated gonads only on the radial canals.

Most of the previously-collected specimens of *Homoeonema platygonon* had broken tentacles close to or at a very short distance from the bell margin. The rarely-seen tentacles have been described as being uniform throughout. In our specimens, as seen above, the tentacles do not have the uniform structure of the other Rhopalonematidae, their structure in fact show some affinities with Halicreatidae tentacles. The genera belonging to this last family

have however very distinct features, quite different of those of *Homeonema*; they have very broad radial canals, a broad and circular manubrium without lips, marginal tentacles of different sizes, structurally all alike and arranged in single series. But each of those tentacles is divided into a soft flexible proximal part and a stiff distal region covered wih cnidocists, a structure close to that observed in *Homoeonema*. Nevertheless, in all its other morphological characters *Homoeonema* is very close to the Rhopalonematidae, so this genus must remain included in this family where it has however a particular situation as much by the position of its gonads as by the structure of its tentacles. This last feature may indicate possible affinities between the Halicreatidae and Rhopalonematidae.

The redescription of *Homoeonema* bring us to modify the definition of the Rhopalonematidae as follows: Trachymedusae with a narrow manubrium; with or without peduncle; without centripetal canals; with 8 (rarely more) narrow radial canals; with a mouth with lips; with gonads either on radial canals, globular, linear, or pendant, or forming a continuous ring around the manubrium and extending outwards along the radial canals; with marginal tentacles evenly distributed, sometimes of two types; each tentacle of uniform structure throughout or divided into a flexible proximal part, devoid of cnidocysts and a distal part that is crowded with cnidocysts; with free, rarely enclosed, marginal sensory clubs.


DISCUSSION

**Mediterranean deep-water hydromedusae**

The numbers and percentages of hydromedusae cited below represent more or less the present-day inventory of deep-water species. At this time, the depth range of many hydromedusae is unknown, some of them may be eurybathic or may even accidentally or exceptionally have been captured in deep-water, and finally, new species are regularly being described.

It emerges from the literature that the Mediterranean Sea contains around 380 species of Hydroidomedusae from which 176 (46%) are represented only by their polyp stage and 204 (54%) by mero- or holopelagic hydromedusae (Boero and Bouillon, 1993; Boero *et al*., in press). Only 41 (20%) of these medusae are known from Mediter-

ranean deep-waters (Table 3). About 90 species of the hydromedusae described in the world have a mesopelagic or a bathypelagic range of distribution (Table 4), this represents about 13% of their total number (about 700). The deep-water Mediterranean hydromedusae fauna comprises thus 45% of the world's described deep-water species.

The hydromedusan fauna of the western Mediterranean is for historical reasons (localisation of the major biological stations and of the main oceanographic surveys) much better known than that of the eastern basin and their data are simply not comparable mainly when the deep-waters are considered. Several papers, however, have been published in the last decade on the composition and distribution of the neritic hydromedusae of the Eastern Mediterranean (Dowidar 1983, 1985; Goy *et al*., 1988, 1991; Lakkis and Zeidane, 1985).

Kramp (1959) assumes that all the species which have been found in the Alborán sea also occur in other parts of the Mediterranean. The geographical distribution of the 41 Mediterranean deep-water species is reported in Table 3. It is evident that conclusions that might be extrapolated from such table must be interpreted with caution, the real distribution of most species being more intrinsically linked to ecological and environmental factors than to artificially established geographical regions and historic reports. It emerge nevertheless from a distributional analyse of table 3 that 9 (22%) species can be considered as endemic, that among the 32 non-endemic species, 3 are found merely in the Atlantic, 1 only in the Indo-Pacific and another solely in the Antarctic; that the majority of the 27 remaining species, are present in both Atlantic and Indo-Pacific waters (21 or 78%) and finally that 15 (56%) are among other areas also known from Antarctic and 8 (21%) from cold waters of the Arctic.

The Mediterranean deep-water hydromedusan fauna comprises 8 Anthomedusae (19.5%), 8 Leptomedusae (19.5%), 9 Narcomedusae (22%), 16 Trachymedusae (39%) and no Limnomedusae or Laingiomedusae. The Trachymedusae appears to be the most distinctive group of the Mediterranean deep-water fauna representing 39 % of the species compared to only 6.5% in the epipelagic zone.

At the level of the world-wide hydromedusan deep-water fauna, the percentage of Trachymedusae is almost the same: 41% (See Table 4). The Trachymedusae are also globally the most characteristic group of hydromedusae in the Subantarctic and Antarctic waters (see Bouillon, in press). The Lim-

TABLE 3. – List of the mid- and deep water hydromedusae known from the Mediterranean Sea (41 species).

| Species | Atlantic | Indo-Pacific | Antarctic | Arctic | Mediterranean |
|---|---|---|---|---|---|
| **Anthomedusae:8** | | | | | |
| *Amphinema rubra* | - | - | +A | - | + |
| *Bythotiara murrayi* | + | + | - | - | + |
| *Calycopsis simplex* | + | - | - | +A | + |
| *Eugotea petalina* | - | + | - | - | + |
| *Euphysa aurata* | + | + | - | +A | + |
| *Paragotoea bathybia* | + | - | +A | +AP | + |
| *Rhabdoon singulare* | + | + | - | - | + |
| *Zanclea* sp. | + | + | +P | - | + |
| **Leptomedusae: 8** | | | | | |
| *Barcino foixensis* | - | - | - | - | + |
| *Foersteria antoniae* | - | - | - | - | + |
| *Foersteria araiae* | - | - | - | - | + |
| *Krampella tardanti* | - | - | - | - | + |
| *Krampella dubia* | + | - | - | - | + |
| *Modeeria rotunda* | + | + | +AP | +A | + |
| *Octophialucium funerarium* | + | - | - | +A | + |
| *Teclaia recincolae* | - | - | - | - | + |
| **Narcomedusae: 9** | | | | | |
| *Aegina citrea* | + | + | +AP | + | + |
| *Cunina globosa* | + | + | - | - | + |
| *Cunina simplex* | - | - | - | - | + |
| *Solmaris corona* | + | + | - | - | + |
| *Solmaris flavescens* | + | + | - | - | + |
| *Solmaris leucostyla* | - | - | - | - | + |
| *Solmissus incisa* | + | + | - | - | + |
| *Solmissus albescens* | - | - | - | - | + |
| *Solmundella bitentaculata* | + | + | +AP | - | + |
| **Trachymedusae: 16** | | | | | |
| *Arctapodema australis* | - | + | +P | - | + |
| *Arctapodema amplum* | + | + | +AP | - | + |
| *Haliscera bigelowi* | + | + | - | - | + |
| *Haliscera racovitzae* | + | + | +AP | - | + |
| *Haliscera conica* | + | + | +AP | - | + |
| *Halitrephes maasi* | + | + | +AP | - | + |
| *Homoeonema platygonon* | + | - | - | - | + |
| *Pantachogon haeckeli* | + | + | +AP | +AP | + |
| *Pantachogon militare* | + | + | +A | - | + |
| *Persa incolorata* | + | + | - | - | + |
| *Ptychogastria asteroides* | - | - | - | - | + |
| *Ransonia krampi* | + | - | - | - | + |
| *Rhopalonema funerarium* | + | + | - | - | + |
| *Rhopalonema velatum* | + | + | +AP | - | + |
| *Sminthea eurygaster* | + | + | +AP | - | + |
| *Tetrorchis erythrogaster* | + | + | - | - | + |

A= Atlantic sector, P= Pacific sector

| Species | n |
|---|---|
| **found in the Mediterranean only** | 9 |
| **found in the Mediterranean and in the following areas:** | |
| Antarctic | 1 |
| Atlantic | 3 |
| Atlantic and Arctic | 2 |
| Atlantic, Antarctic and Arctic | 1 |
| Atlantic and Indo-Pacific | 9 |
| Atlantic, Indo-Pacific and Antarctic | 9 |
| Atlantic, Indo-Pacific and Arctic | 1 |
| Atlantic, Indo-Pacific, Arctic and Antarctic | 3 |
| Indo-Pacific | 1 |
| Indo-Pacific and Antarctic | 1 |
| Indo-Pacific, Arctic and Antarctic | 1 |

Species present in the Atlantic: 28, in the Indo-Pacific: 25, in the Antarctic 16, in the Arctic 8

nomedusae and Laingiomedusae seem to be apparently absent from Antarctic waters. In the Mediterranean, the percentage of holoplanktonic species is proportionally much higher in the deep-water (61%) than in the epipelagic zones (16%). However, contrary to an opinion often expressed, the deep-water meroplanktonic hydromedusae species are quite numerous (39%), and the Leptomedusae (19.5%) are as abundant as the Anthomedusae (19.5 %). From a global point of view, the deep-water Anthomedusae represent 27 % and the Leptomedusae 17%, and in the epipelagic Mediterranean zone the Anthomedusae are represented by about 48% and the Leptomedusae by only 32%.

It is logical to suppose that the polyp stage of most of the meroplanktonic deep-water hydromedusae species must be bathybenthic, some of them have effectively been dredged at great depths or found in sedimentary traps, others may be epizoic or parasites on other living mesoplanktonic or bathypelagic organisms. The results concerning the Mediterranean deep-water fauna are completely consistent with what is known about the world-wide deep sea hydromedusae fauna, where the holoplanktonic species represent 56 % (41% Trachymedusae + 15% Narcomedusae) of the fauna against (44%) for the meroplanktonic ones (see Table 4).

The world-wide deep-water hydromedusae seem to be restricted to a few families. In the Anthomedusae 35 % belong to the family Pandeidae, a 30 % to the Calycopsidae and 29 % to the Corymorphidae; in the Leptomedusae the families Tiarannidae with 33 % and the Mitrocomidae with 27 % are the most representative. In the Narcomedusae, the families Aeginidae, Cuninidae, and Solmarisidae are almost equally represented and finally in the Trachymedusae 73 % of the deep-water species belong to the Rhopalonematidae, 21.6 % to the Halicreatidae and 5.4 % to the Ptychogastriidae. But, those two last percentages represent 100% of the species in both families, whereas only about 80 % of the Rhopalonematidae occur in deep-water. As in the Mediterranean there are no deep-water Laingio- and Limnomedusae (see also Larson *et al*. 1992) nor are they found in the Antarctic or in Artic waters.

As might be logically expected no bathypelagic Anthomedusae possess ocelli, but this has however not a great meaning because most of them belong to families which normally are devoid of ocelli or which have species with and without ocelli. No Leptomedusae except *Barcino foixensis* (Gili *et al*.,

in press) and *Octophialucium funerarium* (Quoy and Gaimard 1827) have closed velar statocysts, all the other deep-sea species have either open statocysts or cordyli or no visible sense organs at all. Two deep-water Leptomedusae unexpectedly have ocelli *Barcino foixensis* and *Tiaropsidium atlanticum*. This last species having a complex sense organ formed by an open statocyst and an ecto-endodermal ocellus. All of the Narcomedusae have their sense organs in the form of free sensory clubs with an endodermal axis and so have all the deep-water Trachymedusae with exceptions *Rhopalonema velatum*, *R. funerarium* and *Sminthea eurygaster* which are well known to live mainly in upper waters and which have closed ecto-endodermal statocysts. The almost general absence of velar or ecto-endodermal closed statocysts in those deep-water hydromedusae may perhaps have some physiological significance which is not understood at this time.

According to Kramp (1959), the Mediterranean hydromedusan fauna seems as a whole to have distinct Atlantic characters and may be designated as an impoverished Atlantic fauna. Analysis of Table 3 indicates that the Mediterranean deep-water hydromedusan fauna appears to be an impoverished derivative of both Atlantic and Indo-Pacific faunas and present also clear affinities with the Antarctic fauna. It must, however been noted that most of the Mediterranean species inhabiting in the Indo-Pacific also occur in the Atlantic and vice versa and this does not contribute in clarifying the question of the origin of the Mediterranean fauna.

Following Kramp (1968, page 185) "the bathypelagic fauna seems to be an ancient fauna since no less than ten genera of hydromedusae are endemic in the bathypelagic zone, having no representatives in the upper water layers". For this author the origin of this hydromedusan fauna should be found in the Atlantic Ocean from which its distribution should have slowly and gradually extended to the other oceanic basins, no great submarine barriers being present to prevent this kind of expanding distribution (except those bordering the Arctic basins and since 5 MaBP the Gibraltar Strait, see below). This hypothesis could be corroborated by modern oceanographic observations which show that the Indian ocean and Indo-Pacific deep-waters are slowly renewed by admixture of deep Atlantic and Antarctic water masses (Deacon, 1963). It is also well established that the structure and dynamics of the Antarctic Ocean influence the water masses and

TABLE 4. – List of the mid- and deep water hydromedusae recorded world-wide (90 species). Only nominal species have been included. This list could be increased when the species mentioned by Thuesen and Childress (1994) (*Crossota* sp. A, *Pantachogon* sp. A, *Tetrorchis* sp.A, *Aegina* sp. A) and Mills *et al.* (1996) (*Arctapodema* sp.) as sp. will be definitively described. Only references after Kramp (1961) and Bouillon (1985) are given: 1, Margulis (1989), 2, Gili *et al.* (in press); 3, this paper; 4, Gili *et al.* (1998); 5, Larson and Harbison (1990); 6, Thuesen (1993).

| Species | Atlantic | Indo-Pacific | Antarctic | Arctic | Mediterranean |
|---|---|---|---|---|---|
| **Anthomedusae:** | | | | | |
| **(24=27%)** | | | | | |
| *Amphinema krampi* | + | - | - | - | - |
| *Amphinema rubra* | - | - | +A | - | + |
| *Annatiara affinis* | + | + | - | + | - |
| *Bythotiara depressa* | - | + | - | +P | - |
| *Bythotiara murrayi* | + | + | - | - | + |
| *Calycopsis bigelowi* | - | + | - | - | - |
| *Calycopsis borchgrevinki* | - | - | +AP | - | - |
| *Calycopsis nematophora* | - | + | +A | +P | - |
| *Calycopsis simplex* | + | - | - | +A | + |
| *Catablema vesicarium?* | + | + | - | +AP | - |
| *Chiarella centripetalis* | - | + | - | +P | - |
| *Eugotoea petalina* (1) | - | + | - | - | + |
| *Euphysa aurata* | + | + | - | +A | + |
| *Euphysora furcata* | + | + | +A | +A | - |
| *Euphysora gigantea* | + | - | +A | - | - |
| *Heterotiara anonyma* | + | + | - | A | - |
| *Meator rubatra* | - | + | - | +AP | - |
| *Merga reesi* | + | + | - | - | - |
| *Neoturris breviconis* | + | + | - | +AP | - |
| *Pandea rubra* | + | + | +AP | - | - |
| *Paragotoea bathybia* | + | - | +A | +AP | + |
| *Rhabdoon singulare* | + | + | - | - | + |
| *Yakovia polinae* (1) | - | - | + | + | - |
| *Zanclea* spp | + | + | + | - | + |
| **Leptomedusae:** | | | | | |
| **(15= 17%)** | | | | | |
| *Barcino foixensis* (2) | - | - | - | - | + |
| *Chromatonema hertwigi* | - | + | - | - | - |
| *( = probably C. rubrum)* | | | | | |
| *Chromatonema rubrum* | + | + | +AP | - | - |
| *Foersteria antoniae* (3) | - | - | - | - | + |
| *Foersteria araiae* (2) | - | - | - | - | + |
| *Foesteria purpurea* | - | + | - | - | - |
| *Halopsis ocellata* | + | + | + | + | - |
| *Krampella dubia* | + | - | - | - | + |
| *Krampella tardenti* (4) | - | - | - | - | + |
| *Modeeria rotunda* | + | + | +AP | +A | + |
| *Octophialucium funerarium* | - | - | - | +A | + |
| *Ptychogena lactea* | - | + | + | +AP | - |
| *Teclaia recincolae* (2) | - | - | - | - | + |
| *Tiaropsidium atlanticum* | + | - | - | - | - |
| *Tima saghalinensis* | - | - | - | +P | - |
| **Narcomedusae:** | | | | | |
| **(14=15%)** | | | | | |
| *Aegina citrea* | + | + | +AP | + | + |
| *Aeginopsis laurentii* | - | - | - | +AP | - |
| *Aeginura grimaldii* | + | + | +P | - | - |
| *Cunina duplicata* | + | + | +AP | - | - |
| *Cunina globosa* | + | + | - | - | + |
| *Cunina simplex* (3) | - | - | - | - | + |
| *Pegantha clara* | + | + | +P | - | - |
| *Solmaris corona* | + | + | - | - | + |
| *Solmaris flavescens* | + | + | - | - | + |
| *Solmaris leucostyla* | - | - | - | - | + |
| *Solmissus albescens* | - | - | - | - | + |
| *Solmissus incisa* | + | + | - | - | + |
| *Solmissus marshalli* | + | + | +P | - | - |
| *Solmundella bitentaculata* | + | + | +AP | - | + |

| Species | Atlantic | Indo-Pacific | Antarctic | Arctic | Mediterranean |
|---|---|---|---|---|---|
| **Trachymedusae:** | | | | | |
| **(37=41 %)** | | | | | |
| *Aglantha digitale* | + | + | - | +AP | - |
| *Aglantha elata* | + | + | - | - | - |
| *Amphogona apicata* | + | + | +P | - | - |
| *Amphogona apsteini* | + | + | - | - | - |
| *Arctapodema amplum* | + | + | +AP | - | + |
| *Arctapodema antarctica* | + | + | +P | - | - |
| *Arctapodema australis* | - | + | +P | - | + |
| *Benthocodon hyalinus* (5) | + | + | +P | - | - |
| *Benthocodon pedunculata* | + | + | - | - | - |
| *Botrynema brucei* | + | + | +AP | +A | - |
| *Botrynema ellinorae* | - | - | - | +A | - |
| *Colobonema igneum* | - | + | - | - | - |
| *Colobonema sericeum* | + | + | +AP | - | - |
| *Colobonema typicum* | - | + | - | - | - |
| *Crossota alba* | + | + | - | - | - |
| *Crossota brunnea* | + | + | +AP | - | - |
| *Crossota norvegica* | - | - | - | +A | - |
| *Crossota rufobrunnea* | + | + | - | - | - |
| *Halicreas minimum* | + | + | +P | +P | - |
| *Haliscera bigelowi* | + | + | - | - | + |
| *Haliscera conica* | + | + | +AP | - | + |
| *Haliscera racovitzae* | + | + | +AP | - | + |
| *Halitrephes maasi* | + | + | +AP | - | + |
| *Halitrephes valdiviae= maasi?* | + | + | +AP | - | - |
| *Homoeonema platygonon* | + | - | - | - | + |
| *Pantachogon haeckeli* | + | + | +AP | +AP | + |
| *Pantachogon militare* | + | + | +A | - | + |
| *Persa incolorata* | + | + | - | - | + |
| *Ptychogastria asteroides* | - | - | - | - | + |
| *Ptychogastria polaris* | + | + | +A | +AP | - |
| *Ransonia krampi* | + | - | - | - | + |
| *Rhopalonema funerarium* | + | + | - | - | + |
| *Rhopalonema velatum* | + | + | +AP | - | + |
| *Sminthea eurygaster* | + | + | +AP | - | + |
| *Tetrorchis erythrogaster* | + | + | - | - | + |
| *Vampyrocrossota childressi* (6) | - | + | - | - | - |
| *Voragonema profundicola* | -, | + | - | - | - |

A= Atlantic Sector, P= Indo-Pacific Sector

| Species found in the | n |
|---|---|
| Antarctic | 1 |
| Antarctic and Arctic | 1 |
| Arctic | 4 |
| Atlantic | 2 |
| Atlantic and Antarctic | 1 |
| Atlantic, Antarctic, Arctic and Mediterranean | 1 |
| Atlantic, Arctic and Mediterranean | 2 |
| Atlantic and Indo-Pacific | 7 |
| Atlantic, Indo-Pacific, and Antarctic | 12 |
| Atlantic, Indo-Pacific, Arctic and Antarctic | 5 |
| Atlantic, Indo-Pacific, and Arctic | 5 |
| Atlantic, Indo-Pacific, Antarctic and Mediterranean | 9 |
| Atlantic, Indo-Pacific, Arctic, Antarctic and Mediterranean | 3 |
| Atlantic, Indo-Pacific, Arctic, and Mediterranean | 1 |
| Atlantic, Indo-Pacific, and Mediterranean | 9 |
| Atlantic, and Mediterranean | 3 |
| Indo-Pacific | 7 |
| Indo-Pacific, Antarctic and Arctic | 2 |
| Indo-Pacific, Antarctic and Mediterranean | 1 |
| Indo-Pacific, and Arctic | 3 |
| Indo-Pacific and Mediterranean | 1 |
| Mediterranean | 9 |
| Mediterranean and Antarctic | 1 |

Species present in the Mediterranean 41, in the Atlantic 59, in the Indo-Pacific 64, in the Antarctic 37, in the Arctic 27, endemic to various areas 23

fauna distribution of the other major oceans. Many deep-water hydromedusae are in fact found in the three oceans. But it must been underlined that many Atlantic deep species have not been found in the Mediterranean waters and that this latter area contains many species not known from the Atlantic waters. Historic events have undoubtedly played a major influence in the recruitment of the Mediterranean hydroidomedusan fauna.

In previous geological eras, the Mediterranean landscape was very different from that of the present time. The present Mediterranean Sea is a remnant part of the ancient Tethys Sea, an east-west seaway that lay between Eurasian and African crustal plates during the late Paleozoic era and Mesozoic era. In the beginning of the Cretaceous some 95 Ma BP, during what has been called the Cenomanian, the Mediterranean had connections with the North Sea through the basin of Paris, with the tropical Atlantic through the Morocco Rif zone and with the Indian ocean through Mesopotamia. These connections allowed easy faunal interchanges, which explains the great Indo-Pacific affinities with the eastern Atlantic fauna and contributed to the presence of the numerous circumtropical species found now in the Mediterranean waters (see Boero and Bouillon, 1993), assuming of course that this Tethys fauna could have survived to the dramatic subsequent geological events that affected this area, which seems doubtful.

More likely the "Atlantic, Indo-Pacific" Tethys faunal stock was reintroduced, re-invading, the Mediterranean in the Pliocene after the opening of the Strait of Gibraltar. In the early Miocene (the Burdigalian), about 18 Ma BP ago, the junction with Eurasia and Africa closed the eastern part of the Mediterranean and the only communication left was that with the Atlantic, leading at the same time to isolation of the tropical Indo-Pacific marine fauna province. In the meantime, the Mediterranean was isolated from the Paratethys Sea and the climate became drier and cooler (Cita *et al.*, 1978; Hsü *et al.*, 1978; Montader *et al.*, 1978). In the late Miocene during the Messinian, between 6 and 5 Ma BP, the Mediterranean-Atlantic communication was in turn closed what led to the isolation and near-drying up of the Mediterranean. Perhaps only the deepest parts could retain water and acted as faunal refuge areas. The occurrence of Foraminifera, diatoms, and algal stromatolites in the Messinian bottom sediments indicate that marine conditions remained and that life was still possible during the Messinian crisis. In the late Miocene (late Messinian) the Paratethys (Lago Mare) inundated the eastern Mediterranean and perhaps extended into the western part. Most of the basins and canyons already existed before or during the Messinian crisis. In the beginning of the Pliocene, the opening of the strait of Gibraltar toward 5 Ma BP restored the sea level and permitted again faunal exchanges with the Atlantic. But this shallow strait (320 m depth) certainly acted as a barrier for the penetration of the deep-water fauna.

The majority of the present-day epipelagic hydromedusan species with Atlantic affinities have probably entered and colonised the Mediterranean after the Messinian crisis. After the Pleistocene cooling, north Atlantic species invaded the western Mediterranean where they could represent the presently boreal stock. The Mediterranean hydromedusae have an important endemic contingent (more or less 20%, see Boero and Bouillon, 1993) some of them could be relics of the Tethys. Other could be " false endemics", many of them have been found only once more than hundred years ago and never again in spite of intense investigations in the last decades; some are also of dubious taxonomical value.

The majority of the authors consider that there are few deep-water endemics in the Mediterranean (see Kramp, 1959; Pérès and Devèze, 1963; Pérès, 1985), this assertion reflects more a lack of knowledge and observations than the reality (this study reveals 9 endemics on 41 species, 22%). Among the 9 deep-sea endemic Mediterranean hydromedusae 5 are meroplanktonic and all belong to the Leptomedusae (no deep-water Anthomedusae are endemic), 4 only are holoplanktonic: 3 Narcomedusae and 1 Trachymedusae. It is strange that the Trachymedusae which are the most abundant deep-sea hydromedusae subclass, include only one endemic species in the Mediterranean and that the less-numerous Narcomedusae also holoplanktonic, present 3 endemic species. The development of two of these Narcomedusae is direct which exclude a possible parasitic dependence on other medusae. Most of the deep-water Trachymedusae appears in fact, to be very cosmopolitan.

The origin of the deep-water hydromedusan fauna appears to be complex, some epipelagic eurybathic species could have entered the Mediterranean through the strait of Gibraltar with Atlantic inflowing waters, others could be Atlantic upwelling species carried into the Mediterranean in the same

way and adapted to the Mediterranean deep-water. Kramp (1959), concluded that from the 25 bathypelagic species found in the central part of the Atlantic only 7 entered the Mediterranean through the Strait of Gibraltar; among them 2 are also epipelagic (*Persa incolorata* , *Sminthea eurygaster*) and may have been carried in with the inflowing superficial waters and 5 (*Modeeria rotunda*, *Haliscera conica*, *Ransonia krampi*, *Arctapodema amplum*, *Octophialucium funerarium*) ascended to the surface with Atlantic upwelling waters before entering the Mediterranean and only one *Bythotiara murrayi* appears strictly a bathypelagic species.

Some species may also represent relics of the primitive Tethys fauna having survived to the Messinian crisis, their derived taxa could be responsible for the high level of endemism of the deep-water Mediterranean hydromedusae (which account for 50% of the total Mediterranean endemics). In this case, those species should have sustained a continuous deterioration of their environment and survived very difficult ecological stress. This could probably only have been possible for species with resistant resting stages, like cysts or chitinized stolonal systems. It is interesting to underline that the majority of Mediterranean deep-water endemic hydromedusae belong surprisingly to the meroplanktonic Leptomedusae, which have generally strong protected stolons.

The distribution of the present day genus *Foersteria* is very interesting in that respect: *Foersteria purpurea* is known from British Columbia and California (Pacific), *F. bruuni* has been found in the Indian Ocean and *F. araiae* and *F. antoniae* have been discovered each in a different canyons of the Western Mediterranean. No species of this genus are known from the Atlantic. All of them appear to be closely related and could have developed by specific radiation and vicariance events from a single ancestor present in the Indo-Pacific and the Mediterranean before the Burdigalian period.

The few holoplanktonic deep-water endemic species seem to have a different origin. *Solmissus albescens* is an epipelagic eurybathic species and can be considered as a vicariant, if not conspecific with, *S. marshalli*, found in the Atlantic and the Indo-Pacific (see systematic part), *Ptychogastria asteroides* is a vicariant of *P. polaris*; *Solmaris leucostyla* is also an epipelagic-eurybathic species. For Mayer (1910), it is possible that it is only a variety of *S. flavescens* recorded from Mediterranean, the Atlantic and Indo-Pacific. *Cunina simplex* has been

found only twice in intermediate waters, it is a rather small Narcomedusae which could easily escape observation. All these last species could have entered the Mediterranean after the Messinian crisis. It may of course not been exclude that the ancestors of some endemics species could have been introduced after the Messinian crisis, being restricted to peculiar environments or by ecological factors, salinity, water mass circulation or by submarine geomorphology, due to the presence of crests, ridges and canyons or any other reason. Such species would then become isolated, which may increase their speciation and diversity possibilities.

Like many other zoological groups, the hydroidomedusan fauna is assumed to have nearly completely disappeared, at the transition between the Mesozoic and Cenozoic geological times about 65 Ma BP (Herman, 1979) and van der Spoel (1996) hypothesises a post Cretaceous dispersal of the hydromedusae from two faunal centers, Indo-Malayan and Antarctic. For van der Spoel the present day zoogeographic patterns of Narcomedusae and Trachymedusae seem to originate from an Antarctic fauna, while the other subclasses of hydromedusae show distribution patterns around the Indo-Malayan area, but this hypothesis still needs to be confirmed.

Among the 90 world-wide deep-water Hydromedusae, 23 species are exclusively found in one well defined geographical area (see Table 4). Contrary to the opinion of Kramp (I959) that there are no endemic deep-water hydromedusae in the Indo-Pacific, 7 are exclusively found in this area. Twenty-seven deep-water species have been recorded in Arctic waters. The majority, 18 of them, are meroplanktonic; this represents (44%) of the total deep-water Anthomedusae and Leptomedusae known; only 9 holoplanktonic species are present in the same waters, or 18 % of the deep-water holoplanktonic species known. The inverse appears to be more or less the case in the Antarctic, where from the 37 recorded deep-water hydromedusae only 13 are Antho- and Leptomedusae, or 33% of the total meroplanktonic fauna against, 24 holoplanktonic species, or 47 % of the total deep-water holoplanktonic fauna known.

Globally almost as many deep-water species are recorded from the Atlantic (59) as from the Indo-Pacific waters (64); the latter region is second in the number of endemic species just after the Mediterranean; the percentage of meroplanktonic species is higher in Arctic deep-waters than in the Antarctic

ones where the holoplanktonic species are the most abundant. The presence of the great number of meroplanktonic taxa among Arctic endemics could also be linked to the natural barriers isolating this basin. On a world-wide scale the modern deep-water hydromedusae seem thus to present the same affinities and distribution patterns than those defined above for the Mediterranean deep-water fauna, with the exception of the 7 Indo-Pacific endemics.

Following van der Spoel (1996), the deep-water hydromedusae appear less restricted to specific depth layers and water masses than other taxa and many species are recorded outside of their supposed depth range. However Pagès *et al.* (1996) and Pugh *et al.* (1997) have shown that in Antarctic waters, deep-living species occur in restricted depth ranges. Several deep-water hydromedusae are actually eurybathic being found at almost all depths: *Euphysa aurata*, *Cunina globosa*, *Persa incolorata*, *Rhopalonema velatum*, *Sminthea eurygaster*, *Solmaris corona*, *Solmaris flavescens*, *Solmissus albescens*, *Solmissus marshalli*, *Solmundella bitentaculata,* etc. Many typical bathypelagic hydromedusae, which are more or less eurythermic, are found in shallow depth in upwelling areas (see for instance Bouillon *et al.*, 1986; van der Spoel and Bleeker, 1988; Navas-Pereira and Vannucci, 1991, 1994, for the Indo-Pacific and Bleeker and van der Spoel, 1988; Navas-Pereira and Vannucci, 1994; van der Spoel, 1996 for the Atlantic): *Aeginura grimaldii, Aglanta elata, Annataria affinis, Bytothiara murrayi, Calycopsis borchgrevinki, Crossota alba, Euphysora furcata, Haliscera racovitzae, Halicreas minimum, Halitrephes maasi,* etc. Inversely several species considered as epipelagic have been found in deep-waters: *Aeginopsis laurenti, Aequorea forskalea?, Aglantha digitale, Amphogona apsteini, Benthocodon pedunculata, Cunina duplicata, Foesteria purpurea, Heterotiara anonyma, Pegantha clara, Solmaris leucostyla,* etc. Some species of the Arctic and Antarctic upper layers fauna, relatively tolerant to depth, salinity and oxygen variation, sink at the Arctic or Antarctic convergence's, diffuse into other cold water masses, and live in deep-water in the temperate or tropical zones (tropical or equatorial submergence). These are good indicators of water masses: *Aegina citrea, Botrynema brucei, Calycopsis simplex Colobonema sericeum, Chromatonema rubrum, Crossota brunnea, Halicreas minimum, Octophialucium funerarium, Pantachogon haeckeli, Ptychogena hyperborea,* etc. (see Goy, 1991, 1995; van der Spoel and Bleeker, 1988; Navas Pereira and

Vannucci, 1991, 1994; van der Spoel, 1996). Nevertheless, temperature, salinity, oxygen concentration and trophic factors seem to be determinant in the distribution of deep-water hydromedusae in warm water regions. Other hydromedusae are depth dependent and remain generally bathypelagic: *Arctapodema antarctica, Botrynema ellinorae, Crossota norvegica, Crossota rufobrunnea, Ptychogastria asteroides, Ransonia krampi,* etc.

## CONCLUSIONS

The Mediterranean hydromedusan deep-water fauna contain 41 species which represent (45.5%) of the world-wide deep-sea hydromedusan fauna and 20 % of the total number of Mediterranean hydromedusae. This deep-water hydromedusan fauna is characterised by a large percentage of holoplanktonic species (61%) and especially by the great amount of Trachymedusae (39%). Nevertheless and contrary to the general opinion the percentage of meroplanktonic species is equally high (39 %). The most original feature of this fauna, however, lies in its high degree of endemicity (22%) and in the fact that the majority of the endemic Mediterranean deep-water medusae are meroplanktonic Leptomedusae with a supposed bathybenthonic stage; furthermore, 3 species are Narcomedusae and only one endemic deep-water species, *Ptychogastria asteroides*, is a Trachymedusae.

The origin of the Mediterranean deep-water hydromedusan fauna is complex. Some species may still represent relics of the primitive Tethys fauna that have survived the Messinian crisis, which could partially explain both Indo-Pacific and Atlantic affinities, their derived taxa could be responsible of the high level of endemism of deep-water hydromedusa. In more recent times after the Atlantic reopening, some epipelagic eurybathic taxa could have entered from the Atlantic with the inflowing surface waters of the strait of Gibraltar, others could be Atlantic upwelling species carried in the Mediterranean through the strait and adapted to the Mediterranean deep-waters.

On a world-wide scale the general distribution patterns and affinities of the deep-water hydromedusan fauna are very similar to those seen in the Mediterranean Sea, the deep-water fauna presenting clear affinities with the Indo-Pacific, the Atlantic and the Antarctic. Among the 90 deep-water world-wide hydromedusae, 23 species are endemic: 2

Atlantic; 4 Arctic; 1 Antarctic; 9 Mediterranean and, contrary to the opinion expressed by Kramp (1959), 7 are endemic to Indo-Pacific waters. Most of the Arctic deep-water hydromedusae are meroplanktonic. As many deep-water species are present in the Indo-Pacific than in the Atlantic waters.

The deep-water hydromedusae fauna is largely restricted to a small number of Hydroidomedusae families. In the Anthomedusae, the Calycopsidae and the Pandeidae seem the most typical; in the Leptomedusae the Mitrocomidae and the Tiarannidae are the most abundant and contain the majority of the meroplanktonic endemics, one other Leptomedusae family, the Laodiceidae, is rather well represented; the Narcomedusae families are almost equally represented in deep-water. In the Trachymedusae, the Rhopalonematidae with 73 % are the most distinctive of the subclass and this family contains also the greatest number of deep-water hydromedusan species with about 30 % of their total number. The Ptychogastriidae and Halicreatidae appear to be the most characteristic deep-sea families, as all of their representatives have a deep-water distribution.


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