Cnidae variability in *Balanophyllia europaea* and *B. regia* (Scleractinia: Dendrophylliidae) in the NE Atlantic and Mediterranean Sea*

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SUMMARY: Traditionally and for practical reasons, skeleton structure has been the main source of taxonomic characters for scleractinian systematics, whereas information from soft tissues has been comparatively neglected. However, skeleton variability may leave species identification uncertain. The use of characters from soft tissues (e.g. polyp anatomy, cnidae size) is routine in the study of other ("soft") hexacorallian orders. This contribution aims to determine whether cnidae characters are useful in taxonomic studies of scleractinians. The cnidae composition of two congeneric species—*Balanophyllia europaea* (Risso, 1826) and *Balanophyllia regia* Gosse, 1860—have been studied throughout a wide geographical area. The data obtained show consistent qualitative and quantitative differences between the two species. This study shows that the cnidae characters can be useful taxonomic criteria for distinguishing congeneric species.

Key words: Scleractinia, *Balanophyllia*, cnidome, taxonomy, geographical variability.

RESUMEN: VARIABILIDAD EN LOS CNIDOCISTOS DE *BALANOPHYLLIA EUROPAEA* Y *B. REGIA* (SCLERACTINIA: DENDROPHYLLIIDAE) EN EL ATLÁNTICO NORDESTE Y MEDITERRÁNEO. – Tradicionalmente, y por razones prácticas, la estructura del esqueleto ha sido la fuente principal de caracteres en la sistemática de escleractinias, mientras que la obtención de información a partir de los tejidos esta prácticamente desatendida. Sin embargo, la variabilidad del esqueleto puede resultar en identificaciones dudosas. El uso de caracteres a partir de la parte orgánica (e.g. anatomía del pólipo, dimensiones de los cnidocistos) es rutinario en el estudio de otros ordenes de hexacoralarios (blandos). La presente contribución tiene como objetivo evaluar la utilidad en estudios taxonómicos en escleractinias de los caracteres a partir de los cnidocistos. Se estudia la composición de cnidoscistos de dos especies cogenéricas —*Balanophyllia europaea* (Risso, 1826) y *Balanophyllia regia* Gosse, 1860— en una amplia área geográfica. Los datos obtenidos muestran consistentes diferencias cualitativas y cuantitativas entre las dos especies. Este estudio muestra que los caracteres a partir del estudio de los cnidocistos pueden ser criterios taxonómicos útiles para distinguir especies cogenéricas.

Palabras clave: Scleractinia, *Balanophyllia*, cnidoma, taxonomía, variabilidad geográfica.

INTRODUCTION

The cnidae (= cnidocysts) are among the structurally most complex and enigmatic organelles in the animal kingdom (see Burnett *et al.*, 1960; Mariscal, 1974, 1984). They have diverse functions, such as capture of prey, defence, adhesion, construction of mucous tubes and locomotion (see Hand, 1961, Mariscal, 1974; Holstein and Tardent, 1984; Fautin and Mariscal, 1991; Kass-Simon and Scappaticci, 2002). Shostak and Kolluri (1995) speculated about their possible origin in the symbiosis with protists. Referring to the diversity and distribution of cnidae of more than 800 species, these

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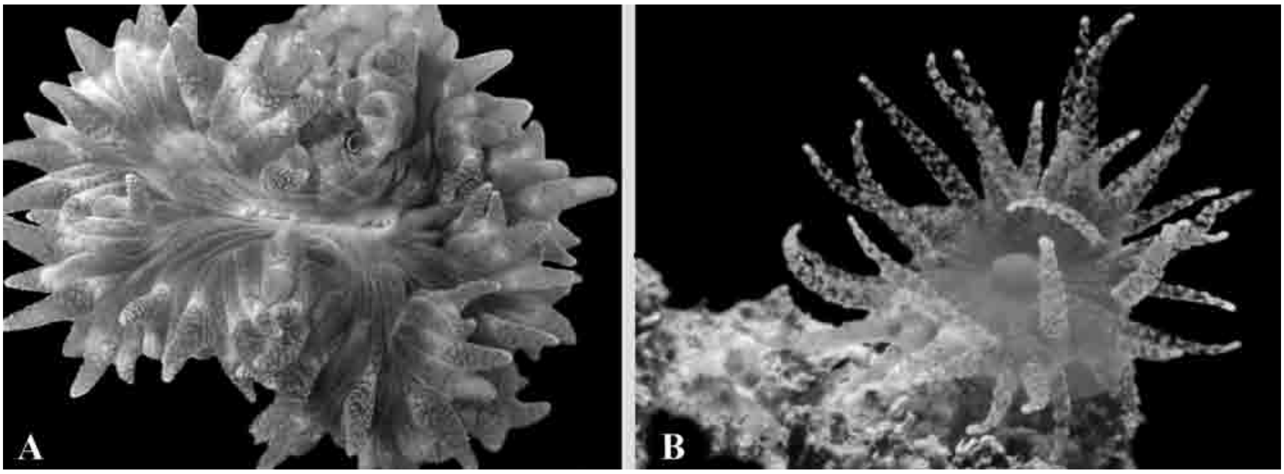

FIG. 1. – Living specimens fully expanded of the two species studied: A, *Balanophyllia europaea* (Risso, 1826) from station E1 (La Caleta); B, *Balanophyllia regia* Gosse, 1860 from a locality close to station R4 (Punta de San García).

authors suggested that the present situation of cnidae was attained in at least two major evolutionary steps.

Three basic types of cnidae are usually distinguished: spirocysts, nematocysts and ptychocysts (Mariscal *et al.*, 1977; Fautin and Mariscal, 1991; Östman, 2000). More recently, a fourth type of cnidae was proposed based on the study of agaricid scleractinians (Pires, 1997), the agaricysts, but for a final acceptation more information on its variability and ultrastructure is needed.

The anthozoans differ from the hydrozoans, schyphozoans and cubozoans by possessing all three basis types of cnidae (see Mariscal, 1984; Östman, 2000). Nematocysts occur in all cnidarians, spirocysts only in hexacorals, and pticocysts only in ceriantharians (see Mariscal, 1984, Fautin and Mariscal, 1991).

Traditionally, cnidarian systematics considered the cnidae (types and size categories) as an important character (e. g. Carlgren, 1900). As for anthozoans, cnidae measurements from different parts of the polyp are commonly used to discriminating characters only in the study of “soft” hexacorals (zoanthids, ceriantharians, corallimorpharians, and actiniarians) (Fautin, 1988; England, 1991).

For scleractinians, the largest hexacorallian order, the main and often only taxonomic character has been the calcareous skeleton, a not fully satisfactory situation (Zibrowius, 1980; Chevalier and Beauvais, 1987; Pires and Pitombo, 1992). The scleractinian skeleton can vary according to physical (e.g. hydrodynamic, depth, sedimentation) or biological (e.g. symbiosis, competition, depredation) environmental conditions (Chevalier and Beauvais, 1987; Zibrowius, 1980). Characters from the study of cnidae were already used by Carlgren (1940; 1945) for the description of scleractinians. Pires (1997) confirmed the potential utility of soft tissues and the diversity of scleractinian cnidae.

Here, we intend to test the constancy of cnidae categories and their distribution in different parts of the polyp from a qualitative and quantitative point of view. This should help to elucidate whether cnidae in scleractinians can be used for taxonomic purposes. Our approach is to study the geographic and specific variability of cnidae in two species of the genus *Balanophyllia* Wood, 1844 (Scleractinia, Dendrophylliidae).

MATERIAL AND METHODS

The shallow-water species *Balanophyllia europaea* (Risso, 1826) and *B. regia* Gosse, 1860 (Fig. 1) are solitary forms, rarely fused forming pseudocolonies (Zibrowius, 1980). *Balanophyllia europaea* is zooxanthellate and lives on rocky shores from near the sea surface to 50 m depth. It occurs throughout the Mediterranean Sea and also on the Atlantic coast of southwest Spain in Cádiz (Zibrowius, 1980, 1983). *Balanophyllia regia* is azooxanthellate and lives on rocky shores from very shallow water down to 25 m depth. It occurs in the Mediterranean Sea and northeastern Atlantic from southeast Ireland and England to Morocco and the Canary Islands (Zibrowius, 1980).

The material studied here was collected by SCUBA diving in various areas of the northeast Atlantic and Mediterranean Sea (Fig. 2 and Table 1). The samples were fixed in 4% formalin before being

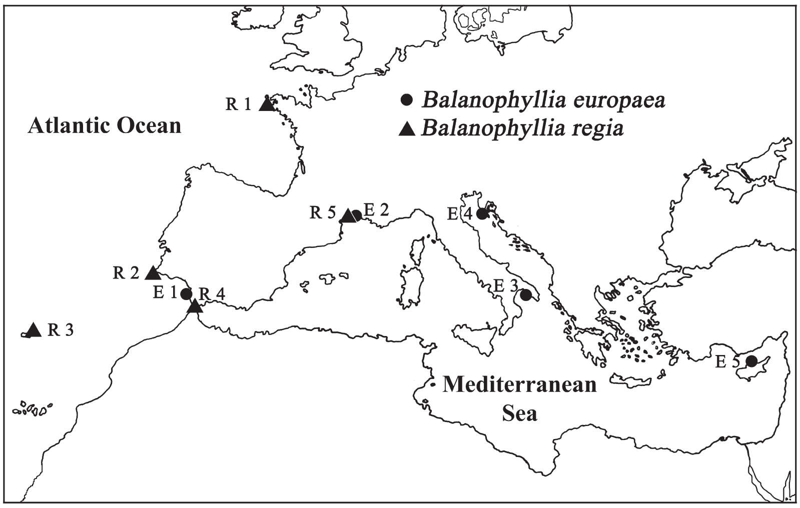

FIG. 2. – Map indicating the sampling stations of *Balanophyllia europaea* (E1 to E5) and *Balanophyllia regia* (R1 to R5), see Table 1 for more details.

transformed into 70% ethanol. From each sampling station the three largest specimens were used. They were decalcified using a 10% solution of formic acid in 4% formalin. For the examination of the cnidae, squash preparations of tissues from different parts of the polyps (columella, pharynx, mesenterial filament, tentacles and scapus) were made. Undischarged cnidae were measured using a Leica DMLB with Nomarski interference contrast optics at maximum magnification following the usual methods of observation (Godknecht and Tardent, 1988).

As a routine, at least 15 undischarged capsules of each cnidae type and category present in the different parts of each polyp studied were measured. This resulted in a minimum of 45 measurements for each cnida (category and type) at each sampling location. For each sampled population, the average, standard deviation, maximum and minimum value of each cnida were calculated. Frequencies are subjective impressions based on squash preparations. The following codes are used in the tables: +++ = very common, ++ = common, + = quite common, - = uncommon, and — = rare.

TABLE 1. – List of sampling stations and collecting data, see also Figure 2.

Code	Collecting data
Balanophyllia europaea	
E1	La Caleta, Cádiz, Spain, Atlantic, 7 m, 18 Jun 1998.
E2	Bandol, Galère beach, ca. 40 Km East from Marseille, France, Mediterranean, 3 m, 12 Sep 1999.
E3	Porto Cesareo, Italy, Mediterranean, 8 m, 6 Feb 2000.
E4	Vrsar, Istra, Croatia, Mediterranean, 5 m, 1 Jul 1999.
E5	Maremonte, Northern Cyprus, Mediterranean, 2-3 m, 18 Nov 1998.
Balanophyllia regia	
R1	Ile de Croix, France, Bretagne, Atlantic, 20 Mar 1999.
R2	Sagres, Algarve, Portugal, Atlantic, Sept 1986.
R3	Punta da Cruz, Madeira, Atlantic, 6 m, 1 Sept 1998.
R4	Punta de San García, Cádiz, Spain, Strait of Gibraltar, 2-5 m, 25 Jul 1998.
R5	Marseille, France, Mediterranean, 10 May 1999.

For both species the relationships between the sampling stations were obtained by a coefficient measuring similarity (or dissimilarity). The Bray-Curtis index (Bray and Curtis, 1957) , which is not a function of joint absences, was chosen for this purpose. Stations were classified into groups (using the triangular matrix of similarity obtained between every pair of stations) by hierarchical agglomerative clustering, with group-average linking (Sneath and Sokal, 1973), or by mapping the station inter-relationships in an ordination by non-metric multidimensional scaling (MDS) (Kruskal and Wish, 1978). All these analyses were carried out with the NTSYST-PC software (Rohlf, 1993).

In the text, figures, and tables, the following abbreviations are used: ΔS = size increment; $\Delta\bar{X}$ = average increment; = average; SD = standard deviation; H, holotrichs; Bs, basitrichs; M*p*m, microbasic *p*-mastigophores; Sp, spirocysts.

RESULTS

The following results are based on the study of more than 8000 undischarged capsules. Two types of cnidae were recorded in the two species of *Balanophyllia*: spirocysts and nematocysts. Following Weill's (1934) nomenclature and Carlgren's (1940) amendments, the nematocysts observed were sorted into three types: holotrichs, basitrichs , and microbasic *p*-mastigophores. In each type, different categories were recognised according to differences in size range and differences in the relative length of capsules and shafts.

Composition and geographical variability of the cnidome of *Balanophyllia europaea*

In *B. europaea* we were able to find a total of 9 categories of nematocysts (three basitrichs, three holotrichs and three microbasic *p*-mastigophores) and one category of spirocysts. The cnidome composition and size of cnidae present in different parts of the polyps were found to be constant throughout the sampling area (Figure 3, 4 and Table 2). The subjective frequency of each cnida type was similar at all stations. Despite this relative constancy, the subjective frequency of each cnida varied from rare (—; e.g. basitrichs 1 in the scapus) to very common (+++; e.g. spirocysts in the tentacles).

The average increment of each type of cnida (comparing the five sampling stations) varied independently of the size increment in that cnida. Thus, cnidocysts with a wide size range showed both slight and great differences (e.g. the holotrichs 3 from the columella with a ΔS of 42.4 μm showed a $\Delta\bar{X}$ of 1.7 μm, while the holotrichs 3 from the scapus with a ΔS of 46.3 μm showed a $\Delta\bar{X}$ of 6.8 μm), and cnidocysts with a medium size range showed a similar tendency (e.g. the holotrichs 2 from the mesenterial filaments with a ΔS of 22.2 μm showed a $\Delta\bar{X}$ of 2.43 μm, while the holotrichs 2 from the tentacles with a ΔS of 20.2 μm showed a $\Delta\bar{X}$ of 7.63 μm). The most restricted case was that of the holotrichs 1 in the scapus, with a ΔS of 7.12 μm which showed a $\Delta\bar{X}$ of 0.7 μm. With regard to the SD, as a general rule the values observed at the sampling stations overlapped in each cnida type (see Fig. 4). In a few cases (basitrichs 3 and holotrichs 2 of tentacles, and holotrichs 2 of pharynx), the SD showed slight differences, producing a wide range at sampling station level. However, in all cases size range widely overlapped.

Composition and geographical variability of the cnidome of *Balanophyllia regia*

In *B. regia* we were able to find a total of 8 categories of nematocyst (three basitrichs, three holotrichs and two microbasic *p*-mastigophore) and one category of spirocyst. As in *B. europaea*, the cnidome composition and size of cnidae present in different parts of the polyps was found to be constant throughout the sampling area (Table 3 and Figs. 3, 4). The subjective frequency of each cnida type was similar at all stations. The subjective frequency of cnida types was highly unequal, varying from rare (—; e.g. basitrichs 1 in the mesenterial filaments) to very common (+++; e.g. microbasic *p*-mastigophores 3 in the tentacles).

As in *B. europaea*, the average increment of each type of cnida (comparing the five sampling stations) varied (in most cases) independently of the size increment in that cnida. This trend was more accentuated in medium sized cnidocysts than in larger ones. Thus, cnidocysts with a wide size range showed both slight and relatively great differences (e.g. the holotrichs 3 from the columella with a ΔS of 32.3 μm showed a $\Delta\bar{X}$ of 3.67 μm, while the holotrichs 3 from the scapus with a ΔS of 50.5 μm showed a $\Delta\bar{X}$ of 6.93 μm), and cnidocysts with a medium size range showed a behaviour more similar to *B. europaea* (e.g. the basitrichs 3 from the tentacles with a ΔS of 13.6 μm showed a $\Delta\bar{X}$ of 2.83 μm, while the basitrichs 2 from the mesentrial filaments with a ΔS of 13.1 μm showed a $\Delta\bar{X}$ of 5.6 μm). The cases with a short size range (holotrichs 1 from scapus, mesenterial filaments, and columella) showed a similar tendency with a ΔS between 7.62-7.12 μm and a $\Delta\bar{X}$ between 2.53-2-24 μm. With regard to the SD, as a general rule the values of the SD at the sampling stations overlapped in each cnida type (see Fig. 4). Only the holotrichs 1 (from scapus, mesenterial filaments, and columella), and basitrichs 2 (from the mesenterial filaments) showed slight differences between the sampling stations. However, in all cases the size range overlapped.

Comparison between the cnidae of *B. europaea* and *B. regia*

The sets of cnidae observed in *B. europaea* and *B. regia* differ qualitatively and quantitatively. In B. europaea, 9 categories of nematocysts and 1 of spirocysts were identified, whereas B. regia had only 8 categories of nematocysts and 1 of spirocysts. The additional category exclusive of *B. europaea* was the microbasic *p*-mastigophores 1 present in the scapus with a subjective frequency of common (++) (see Fig. 5 and Table 4). Another marked difference was that of distribution of basithichs 1, common to both species of *Balanophyllia*. In *B. europaea* this

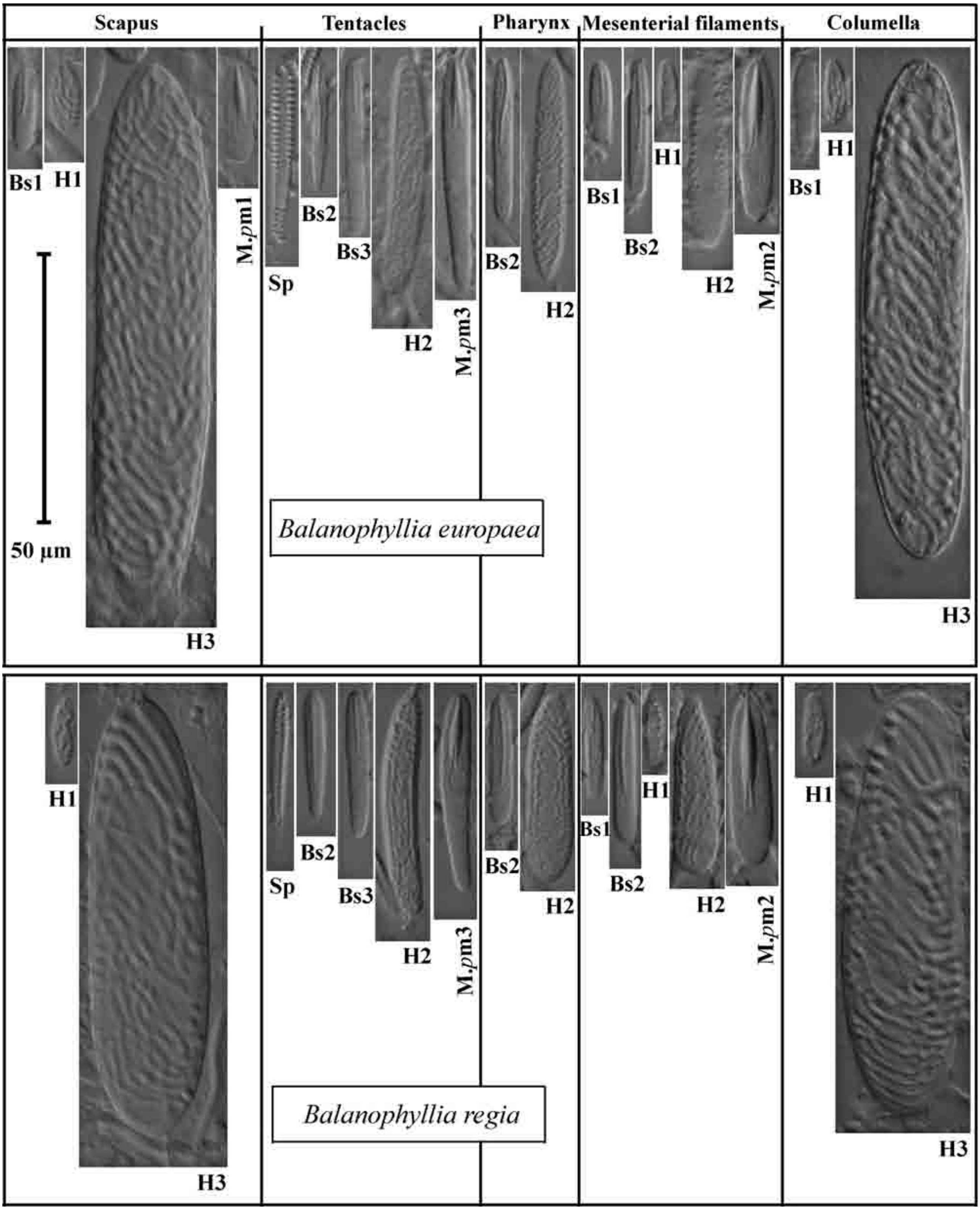

FIG. 3. – Cnidae of *Balanophyllia europaea* and *Balanophyllia regia*. See text and Tables 2 and 3 for explanation. Scale bar: 50 μm.

cnida was present in the scapus, mesenterial filaments and columella, whereas in *B. regia* it was found only in the mesenterial filaments.

Most of the cnidae common to both species showed slight differences in average and size range (see Fig. 5 and Table 4). As a general rule, the aver-

TABLE 2. – Average, standard deviation, range and subjective frequency of the cnidae of *Balanophyllia europaea*. Each sampling station (abbreviation as Table 1, E1 to E5) is considered separately. From each sampling station three individuals are studied.

	Station	Spirocyst	Basitrich 1	Basitrich 2	Basitrich 3	Holotrich 1	Holotrich 2	Holotrich 3	Mic. *p*-mastigophore 1	Mic. *p*-mastigophore 2	Mic. *p*-mastigophore 3
Scapus	**E1**		16.2±2.87 x 3.81±0.47 (11.1-24.2 x 2.5-5) [-]			11.5±1.1 x 4.02±0.46 (10.1-14.1 x 3-5) [+++]		91±7.11 x 9.9±1.39 (72.7-103 x 17.2-24.2) [++]	17.8±1.59 x 5.12±0.6 (15.2-21.2 x 4-7) [+++]		
	E2		13.7±1.62 x 3.47±0.58 (10.1-18.2 x 2.5-5) [-]			10.9±1.27 x 3.5±0.57 (9-13.1 x3-5) [++]		93.46±8.46 x 20.1±1.4 (78.8-112 x 16.2-22.2) [++]	18.16±1.2 x 4.87±0.52 (15.2-21.2 x 3.5-6) [++]		
	E3		15.7±1.15 x 3.67±0.31 (13.1-18.2 x 3-4) [-]			10.83±0.97 x 3.88±0.5 (8-12.1 x 3-5) [+++]		92.06±6.76 x 19.56±1.5 (74.7-109 x 16.2-22.2) [++]	19.73±1.41 x 5.67±0.58 (16.2-22.2 x 4-7) [++]		
	E4		14.53±1.31 x 3.91±0.36 (12.1-18.2 x 3-5) [-]			11.2±1.23 x 3.95±0.43 (9-15.2 x 3-5) [+++]		89.16±7.54 x 20.06±1.25 (74.7-108 x 16.2-22.2) [+]	19.4±1.69 x 5.58±0.98 (16.2-24.2 x 4.5-6.6) [++]		
	E5		14.26±1.47 x 3.74±0.35 (12.1-16.2 x 3-4) [—]			11.46±1.19 x 3.64±0.4 (8-14.1 x 3-4.55) [++]		86.66±9.43 x 19.26±1.5 (65.7-102 x 15.2-22.2) [++]	17.8±2.16 x 5.41±0.65 (14.1-23.2 x 4-7) [++]		
Tentacles	**E1**	27.4±4.66 x 3.67±0.46 (18.2-34.3 x 3-4) [+++]		25.43±2.33 x 3.05±0.28 (20.2-29.3 x 2.5-3.5) [+]	28.6±2.46 x 3.82±0.4 (22.2-33.3 x 3-5.6) [-]		40.1±3.75 x5.56±0.58 (32.3-48.5 x 4-7) [+]				36.56±3.63 x 4.67±0.41 (29.3-44.4 x 4-5) [+++]
	E2	26.8±3.65 x 3.71±0.42 (19.2-33.3 x -3-4) [+++]		23.86±2.28 x 2.76±0.33 (18.2-28.3 x 2-3) [++]	24.34±2.47 x 3.12±0.31 (18.2-30.3 x 2.5-4) [+]		37.13±3.01 x 5.74±0.5 (28.3-42.4 x 4.5-7) [-]				35.9±3.06 x 4.6±0.51 (30.3-42.4 x 4-6) [++]
	E3	32.2±4.52 x 3.73±0.54 (20.2-40.4 x 2.5-5) [+++]		25.43±2.51 x 3.06±0.31 (20.2-31.3 x 2-4) [+]	30.26±2.42 x 3.53±0.39 (23.2-34.3 x 3-4) [-]		42.66±2.83 x 5.7±0.46 (35.4-47.5 x 4-6.6) [-]				38.83±2.63 x 4.9±0.38 (34.3-45.5 x 4-6) [+++]
	E4	29.66±4.24 x 3.76±0.48 (13.1-34.3 x 2.5-4.5) [+++]		23.7±2.43 x 2.96±0.3 (19.2-29.3 x 2.5-3.5) [++]	28.96±2.61 x 3.52±0.36 (23.2-33.3 x 3-4) [+]		41.13±2.49 x 5.86±0.5 (36.4-46.5 x 5-7) [-]				36.6±2.85 x 4.83±0.35 (31.3-42.4 x 4-5.5) [+++]
	E5	27.9±2.78 x 4.15±0.56 (23.2-33.3 x 3-5) [+++]		22.76±2.51 x 3.27±0.26 (19.2-34.3 x 3-3.5) [-]	24.2±2 x 3.64±0.37 (19.2-27.3 x 3-4) [—]		35.03±2.48 x 5.51±0.4 (29.3-40.4 x 5-6.6) [-]				32±2.94 x 5.2±0.43 (26.3-39.4 x 4.5-6) [+++]
Pharynx	**E1**			28.06±2.62 x 3.7±0.6 (22.2-33.3 x 3-5) [++]			36.53±3.5 x 6.43±0.61 (29.3-44.4 x 5-8) [++]				
	E2			28±2.91 x 3.48±0.39 (21.2-36.4 x 3-4) [+++]			33.33±3.36 x 5.96±0.5 (24.2-40.4 x 5-7) [++]				
	R3			29.36±3.67 x 3.67±0.41 (18.2-38.4 x 3-4) [+++]			38.76±3.61 x 6.55±0.7 (30.3-49.5 x 6-9) [+++]				
	E4			27.33±3.18 x 3.34±0.36 (20.2-34.3 x 3-4) [+++]			34.1±3.54 x 6.38±0.69 (27.3-42.4 x 5-8) [++]				
	E5			23.76±2.62 x 3.55±0.39 (19.2-29.3 x 3-4) [++]			30.7±3.17 x 6.48±0.61 (25.3-39.4 x 5-7.6) [+++]				
Mesenterial Filaments	**E1**		13.5±1.39 x 3.75± 0.32 (11.1-16.2 x 3-4.5) [+]	22.33±1.87 x 3.95±0.45 (17.2-25.3 x 3-4.5) [+]		11.74±1.92 x 3.85±0.54 (8-15.2 x 3-5) [+]	30.5±3.28 x 6.73±0.73 (19.2-36.4 x 6-9) [+]			27.96±2.12 x 6.29±0.62 (23.2-33.3 x 5-8) [+++]	
	E2		13.83±1.71 x 3.48±0.37 (11.1-18.2 x 3-4.5) [+]	24.83±2.61 x 3.69±0.47 (20.2-31.3 x 3-4) [+]		10.42±1.05 x 3.62±0.41 (8-13.1 x 3-4) [++]	32.03±4.4 x 6.59±0.66 (19.2-41.4 x 5-8) [-]			27.76±1.93 x 5.99±0.61 (23.3-34.3 x 5-7) [++]	
	E3		13.83±1.92 x 3.93±0.4 (10.1-20.2 x 3-4.5) [+]	23.86±1.78 x 3±0.33 (19.2-28.3 x 3-4.5) [-]		11.8±1.32 x 3.65±0.42 (9-17.2 x 2.5-4) [++]	31.4±2.44 x 6.85±0.57 (26.3-36.4 x 6-8) [-]			30.63±2.58 x 6.36±0.62 (25.3-37.4 x 5-8) [+++]	
	E4		14.2±1.52 x 3.85±0.34 (11.1-18.2 x 3.5-4) [+]	24.9±2.1 x 3.86±0.37 (20.2-29.3 x 3-4.5) [+]		11.3±0.93 x 3.68±0.36 (10.1-14.1 x 3-5) [++]	31.06±2.59 x 6.77±0.5 (27.3-39.4 x 5-7.5) [+]			27.76±1.93 x 6.39±0.54 (24.2-32.3 x 5-7) [+++]	
	E5		12.8±1.28 x 3.89±0.44 (10.1-16.2 x 3-4.5) [+]	20.8±1.97 x 3.87±0.33 (17.2-25.8 x 3-5) [-]		10.53±0.95 x 3.58±0.48 (9-12.1 x 3-4.5) [++]	29.6±2.22 x 7.03±0.33 (24.2-36.4 x 6-7.5) [+]			25.06±2.24 x 6.69±0.8 (21.2-30.3 x 5-8) [++]	
Columella	**E1**		15.63±2.53 x 3.61±0.37 (11.1-22.2 x 3-4) [+]			12.16±1.72 x 4.27±0.61 (9-16.2 x 3-5.5) [+++]		90.9±5.19 x 18.8±1.23 (68.7-101 x 15.2-20.2) [+++]			
	E2		16.06±2.22 x 3.69±0.51 (12.1-21.2 x 2.5-5) [-]			11.83±1.49 x 3.92±0.65 (9-16.2- x 3-5) [+++]		92.06±7.32 x 19.3±2.07 (64.6-107 x 15.2-28.3) [++]			
	E3		14.13±1.83 x 3.95±0.45 (11.1-18.2 x 3-4.5) [-]			12.43±0.98 x 4.27±0.58 (10.1-14.1 x 3-5) [+++]		90.46±6.2 x 19.43±1.92 (77.8-106 x 16.2-24.2) [++]			
	E4		14.46±1.59 x 3.95±0.46 (11.1-19.2 x 3-5) [-]			11.86±0.94 x 4.09±0.39 (10.1-14.1 x 3-5) [+++]		92±7.3 x 22±1.66 (74.7-106 x 19.2-25.3) [++]			
	E5		13.8±1.41 x 3.91±0.45 (11.1-17.2 x 3-5) [+]			11.33±1.33 x 3.99±0.53 (9-15.2 x 3-6) [+++]		90.36±7.61 x 19.86±1.57 (65.7-106 x 15.2-23.2) [++]			

TABLE 3. – Average, standard deviation, range and subjective frequency of the cnidae of *Balanophyllia regia*. Each sampling station (abbreviation as Table 1, R1 to R5) is considered separately. From each sampling station three individuals are studied.

	Station	Spirocyst	Basitrich 1	Basitrich 2	Basitrich 3	Holotrich 1	Holotrich 2	Holotrich 3	Mic. *p*-mastigophore 1	Mic. *p*-mastigophore 2	Mic. *p*-mastigophore 3
Scapus	**R1**					11.3±1.04 x 3.83±0.42 (9-13.1 x 3-5) [++]		76.33±4.75 x 19.03±1.6 (44.4-85.9 x 16.2-22.7) [++]			
	R2					12.13±1.12 x 3.88±0.35 (10.1-15.2 x 3-4.5) [+++]		74±7.99 x 19.8±1.5 (46.5-92.9 x 17.2-22.2) [++]			
	R3					9.64±0.83 x 3.87±0.36 (7.6-11.1 x 3-4.5) [++]		72.6±4.49 x 22.13±1.27 (62.6-81.8 x 19.2-23.7) [++]			
	R4					10.86±1.21 x 4.04±0.53 (9-13.1 x 3-5) [+++]		78±5.1 x 21.1±1.22 (67.7-88.4 x 18.2-23.2) [+]			
	R5					10.96±0.88 x 3.91±0.45 (9-13.1 x 3-5) [++]		79.53±7.13 x 21.4±1.35 (62.6-94.9 x 18.2-25.3) [+]			
Tentacles	**R1**	31.76±3.06 x 3.73±0.45 (37.4-25.3 x 3-5) [+++]		25.53±2.2 x 3.14±0.21 (19.2-30.3 x 3-3.5) [-]	27.73±2.2 x 3.54±0.45 (24.2-32.3 x 3-5) [-]		39.63±2.85 x 5.83±0.6 (32.3-45.5 x 5-7.5) [+]				36.23±2.53 x 4.79±0.37 (30.3-41.4 x 4-5.5) [++]
	R2	28.46±3.57 x 3.93±0.74 (37.4-21.2 x 3-5) [+++]		22.56±1.64 x 3.33±0.38 (17.2-25.3 x 2.5-4.5) [++]	27.6±2.37 x 3.79±0.38 (22.7-32.3 x 3-4.5) [+]		39.7±3.05 x 6.82±0.8 (33.3-47.5 x 5-8) [+]				34.5±3.29 x 5.69±0.67 (26.3-41.9 x 3-4.5) [+++]
	R3	26.16±2.61 x 3.69±0.41 (31.3-19.2 x 3-5) [+++]		20.56±2.13 x 3.06±0.27 (16.2-24.2 x 2.5-4) [-]	24.9±2.38 x 3.49±0.41 (19.2-29.3 x 2.5-4) [++]		34.06±3.65 x 6.92±0.8 (26.3-41.4 x 4.5-8) [+]				30.76±2.3 x 5.21±0.54 (25.3-35.4 x 4-6) [++]
	R4	26.56±2.71 x 3.67±0.41 (31.3-20.2 x 2.5-4) [+++]		21.96±2.01 x 3.18±0.35 (17.2-27.3 x 2.5-4) [+]	27.46±2.74 x 3.72±0.4 (23.2-32.8 x 3-4.5) [+]		37.03±3.2 x 6.71±0.62 (30.3-43.4 x 5-8) [++]				32.9±3.3 x 5.5±0.69 (27.3-40.4 x 4-6.5) [++]
	R5	28.4±3.83 x 3.71±0.52 (35.4-20.2 x 2.5-5.5) [+++]		21.93±1.72 x 3.21±0.36 (18.2-25.3- x 2.5-4) [+]	25.43±2.12 x 3.78±0.43 (21.2-30.3 x 3-4.5) [-]		36.86±4.14 x 6.83±0.9 (29.3-45.5 x 5.5-8.5) [++]				33±4.37 x 5.42±0.7 (26.3-43.4 x 4-7) [++]
Pharynx	**R1**			25.53±2.62 x 3.97±0.4 (20.7-32.3 x 3-5) [++]			34.2±2.68 x 6.1±0.44 (27.3-38.4 x 5-7) [++]				
	R2			24.86±1.77 x 4.08±0.41 (21.7-29.3 x 3.5-5) [+++]			32.93±3 x 7.13±0.73 (26.3-37.4 x 6-8.5) [++]				
	R3			22.23±2.11 x 3.82±0.44 (18.2-27.3 x 3-5) [+++]			31.66±1.92 x 7.54±1.3 (27.3-35.4 x 6.5-9) [+]				
	R4			25.4±2.11 x 4.3±0.49 (20.2-30.3 x 3-5) [++]			32.16±2.08 x 7.81±0.6 (27.3-36.4 x 6.5-9) [+]				
	R5			23.3±4.41 x 4.19±0.41 (16.2-28.3 x 3.5-5) [+++]			34.03±3.25 x 7.96±0.6 (28.3-40.4 x 6.5-9) [++]				
Mesenterial Filaments	**R1**		16.43±1.09 x 3.51±0.36 (14.1-18.2 x 3-4) [-]	24.93±1.79 x 3.99±0.3 (20.2-28.3 x 3-4.5) [-]		12.13±0.97 x 3.59±0.34 (10.1-14.1 x 3-4) [++]	31.23±1.81 x 5.97±0.4 (28.3-36.4 x 4.5-7) [+]			27.5±1.41 x 6.19±0.47 (24.2-30.3 x 5.5-8.) [+++]	
	R2		18.23±1.45 x 3.59±0.39 (15.2-22.2 x 3-4.5) [+]	23.56±1.27 x 3.94±0.32 (21.2-26.3 x 3-5) [+]		12±0.92 x 3.77±0.32 (10.6-14.1 x 3-4.5) [+]	29.76±2.06 x 6.98±0.7 (25.8-35.4 x 5.5-9) [-]			26.76±1.46 x 6.8±0.68 (24.2-30.3 x 5.5-8) [+++]	
	R3		14.2±0.94 x 3.26±0.35 (12.6-16.2 x 3-4) [-]	19.33±2.02 x 3.97±0.4 (16.2-24.2 x 3-5) [-]		9.6±0.82 x 3.65±0.43 (8-11.1 x 3-4.5) [++]	26.6±2.06 x 7.17±0.77 (23.2-31.3 x 6-9) [-]			24.53±1.92 x 7.19±0.67 (20.2-29.3 x 6-9) [++]	
	R4		17.76±1.83 x 3.91±0.55 (14.1-22.2 x 3-5.5) [—]	23.56±1.01 x 4.12±0.46 (21.2-25.3 x 3.5-5) [+]		11.5±0.96 x 4±0.42 (10.1-15.2 x 3-5) [++]	30.13±1.54 x 7.66±0.8 (27.3-33.3 x 6-9) [+]			28.93±2.54 x 8.11±0.5 (25.3-35.4 x 7-9) [+++]	
	R5		15.76±1.56 x 3.37±0.4 (13.1-19.2 x 2.5-4) [-]	23.76±2.45 x 3.94±0.32 (19.2-29.3 x 3.5-4.5) [++]		11.06±0.89 x 3.52±0.35 (9-13.1 x 3-4) [+]	30.4±2.87 x 7.36±0.59 (25.3-36.4 x 6-8) [+]			28.93±3.54 x 7.16±0.99 (23.2-39.4 x 5.5-9.6) [+++]	
Columella	**R1**					11.6±1.09 x 3.74±0.4 (9-13.6 x 3-5) [++]		73.93±5.33 x 17.3±1.65 (57.6-84.8 x 15.2-20.2) [++]			
	R2					12.13±1.17 x 4.14±0.46 (10.1-15.2 x 3.5-5) [+++]		73.16±6.41 x 19.3±1.62 (58.6-87.9 x 15.2-22.2) [+]			
	R3					9.89±0.68 x 3.83±0.36 (8-11.1 x 3-4.5) [+++]		71.33±4.78 x 21.16±1.12 (60.6-84.8 x 19.2-23.2) [++]			
	R4					11.2±1.07 x 4.1±0.49 (9-13.1 x 3.5-6) [+++]		73.2±5.43 x 19.56±3.22 (60.6-86.9 x 15.2-23.2) [-]			
	R5					11.46±1.1 x 4.14±0.46 (9-14.1 x 3.5-5) [+++]		75±6.93 x 21.5±1.18 (55.6-85.9 x 19.2-23.7) [+]			

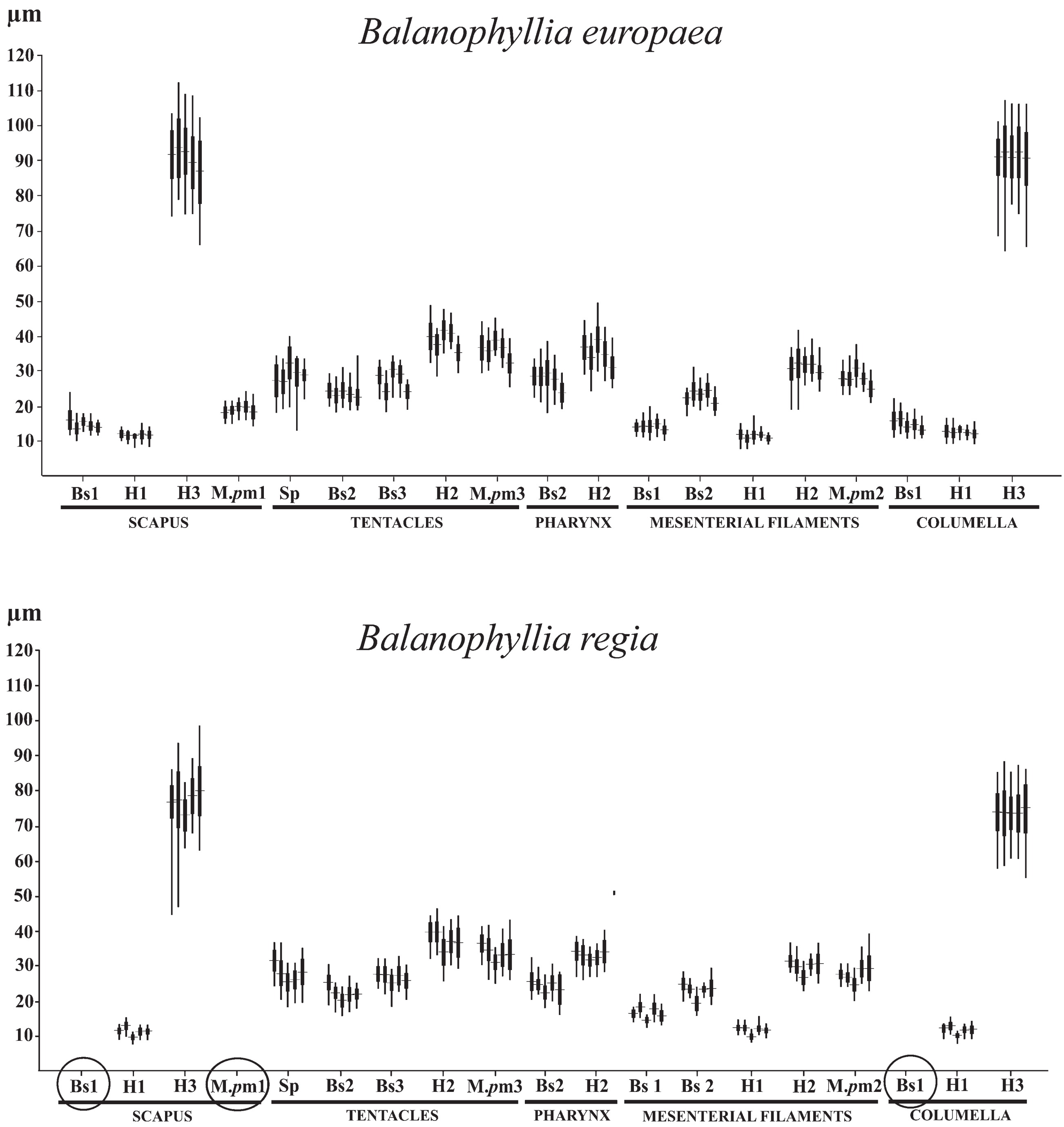

FIG. 4. – Cnidae composition, range, average and standard deviation of *Balanophyllia europaea* and *Balanophyllia regia*. Each cnidae is represented by the data corresponding to the five sampling stations in Table 1 and Figure 2. See also text, Figure 3 and Table 2 and 3 for explanation. The cnidae in both species are listed in the same order. Notice that in *B. regia* , those cnidae absent (in comparison with *B. europaea*) are encircled. The gap is maintained for the purpose of comparison.

age and size range reached higher values in *B. europaea* than in *B. regia*, the only exception being the basitrichs 1 from the mesenterial filaments. This tendency observed for holotrichs 3 in the scapus and columella can be used to distinguish between the two species.

In the scapus, the holotrichs 3 of *B. europaea* had a average range between 86.66 μm (E 5, Cyprus) and 93.46 μm (E 2, Marseille), with an average considering all the sampling stations of 90.47 μm; the size range of this cnida considering all sampling stations varied from 112 to 65.7 μm.

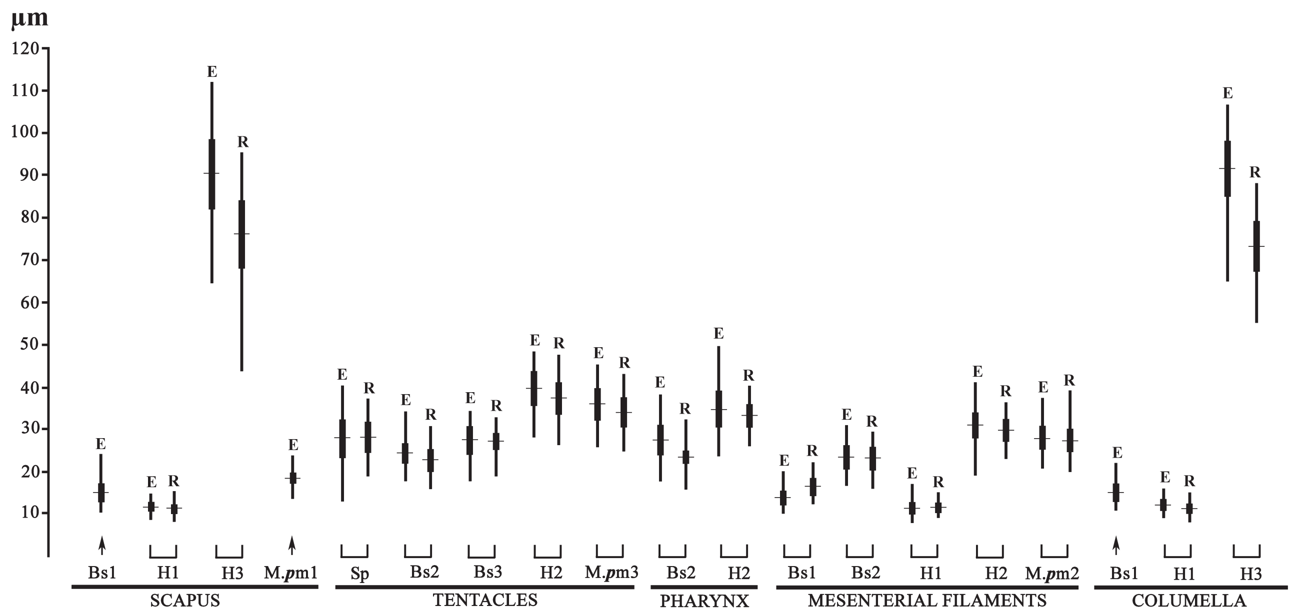

FIG. 5. – Cnidae composition, range, average and standard deviation of *Balanophyllia europaea* and *Balanophyllia regia*. For each species all the data from the different sampling stations have been considered. Notice that for each cnidae type the data of *B. europaea* (E) and *B. regia* (R) are represented together forming a pair, except for those cnida present only in *B. europaea*.

In *B. regia* this cnida had an average range between 72.6 μm (R 3, Madeira) and 79.53 μm (R 5, Marseille), with an average considering all the sampling stations of 76.09 μm; the size range of this cnida considering all sampling stations varied from 94.9 to 44.4 μm (data obtained from Table 2 and 3).

In the columella, the holotrichs 3 of *Balanophyllia europaea* had a average range between 90.36 μm (E 5, Cyprus) and 92.06 μm (E 2, Marseille), with an average considering all the sampling stations of 91.15 μm; the size range of this cnida considering all sampling stations varied from 107 to 64.6 μm. In *B. regia* this cnida had an average range between 71.33 μm (R 3, Madeira) and 75 μm (R 5, Marseille), with an average considering all the sampling station of 73.31 μm; the size range of this cnida considering all sampling stations varied from 87.9 to 55.6 μm.

The more evident differences found between the two species of *Balanophyllia* were those of composition (= cnidome) and nematocyst size range. But there were also slight differences with respect to the subjective frequency of some cnidae. For example, the holotrichs 2 from the tentacles were more abundant in *B. regia* (+) than in *B. europaea* (-), whereas the basitrichs 2 from the mesenterial filaments were more abundant in *B. europaea* (+) than in *B. regia* (-) (see Table 4).

Sample grouping based on cnidae size range in *B. europaea* and *B. regia*

For the present grouping analyses we did not include the qualitative differences between the two species as mentioned above. Including these differences is expected to increase the distance between the set of stations of both species, and to hide the possible relationships between the sampling stations of each species. For the following analyses we used the average at each sampling station of the length of cnida. We obtained a data matrix with 10 columns (5 stations of *B. europaea* labelled E1 to E5; and 5 stations of *B. regia* labelled R1 to R5) and 16 files (cnidae categories common in both species).

In Figure 6, Cluster analysis using the Bray-Curtis index for similarity shows two main groups corresponding to each of the *Balanophyllia* species studied in this paper. Three-dimensional MDS ordination was performed using the similarities between samples (Fig. 6). This MDS-3D also shows the separation between the sampling stations in two subgroups in agreement with the two species analysed.

The sampling stations of *B. europaea* are not clearly related according to geographical proximity, with a higher similarity between E1 and E4 and a progressive differentiation between the other ones up to E5 (Cyprus), which is also the most distant one.

TABLE 4. – Average, standard deviation, range and subjective frequency of the cnidae of *Balanophyllia euroapea*

	Spirocyst	Basitrich 1	Basitrich 2	Basitrich 3	Holotrich 1
B. europaea					
Scapus		14.87±1.96 x 3.72±00.51 (10.1-24.2 x 2.5-5) (—)			11.18±1.18 x 3.8±0.6 (8-15.2 x 3-5) (+++)
Tentacles	28.79±4.43 x 3.8±0.56 (13.1-40.4 x 2.5-5) (+++)		24.23±2.61 x 3.02±0.33 (18.2-34.3 x 2-4) (+)	27.27±3.43 x 3.52±0.39 (18.2-34.3 x 2.5-5.5) (-)	
Pharynx			27.3±3.54 x 3.54±0.57 (18.2-38.4 x 3-5) (++)		
Mesenterial Filaments		13.63±1.63 x 3.78±0.42 (10.1-20.2 x 3-4.5) (+)	23.34±2.6 x 3.67±0.44 (17.2-31.3 x 3-5) (+)		11.15±1.4 x 3.67±0.6 (8-17.2 x 2.5-5) (++)
Columella		14.81±2.12 x 3.82±0.49 (11.1-22.2 x 2.5-5) (-)			11.92±1.36 x 4.1±0.6 (9-16.2 x 3-6) (+++)
B. regia					
Scapus					10.97±1.34 x 3.9±0.51 (7.5-15.2 x 3-5) (+++)
Tentacles	28.26±3.73 x 3.74±0.61 (19.2-37.4 x 2.5-5.5) (+++)		22.5±2.54 x 3.18±0.35 (16.2-30.3 x 2.5-4.5) (+)	26.62±2.64 x 3.66±0.43 (19.2-32.8 x 2.5-5) (-)	
Pharynx			23.26±3.08 x 4.07±0.43 (16.2-32.3 x 3-5) (+++)		
Mesenterial Filaments		16.47±2 x 3.52±0.4 (12.6-22.2 x 2.5-5.5) (-)	23.02±2.6 x 3.99±0,4 (16.2-29.3 x 3-5) (-)		11.25±1.28 x 3.7±0.37 (9-15.2 x 3-5) (++)
Columella					11.25±1.27 x 3.99±0.46 (8-15.2 x 3-6) (+++)

B. regia shows a different pattern, with Atlantic and Mediterranean locations grouping separately. The station R4 (Punta de San García, Strait of Gibraltar) is grouped with R5 (Marseille, France) rather than with R2 (Sagres, southern Portugal), which is geographically closer than the French location. The geographically most isolated station (R3, Madeira) is also the most dissimilar one.

DISCUSSION

The characteristics of the cnidome, i.e. the composition and size range cnidae in different parts of the polyp, are not currently used in scleractinian taxonomy. Matthai (1914, 1928) was aware of the presence of different types of nematocysts in corals and included them for characterising species. There are

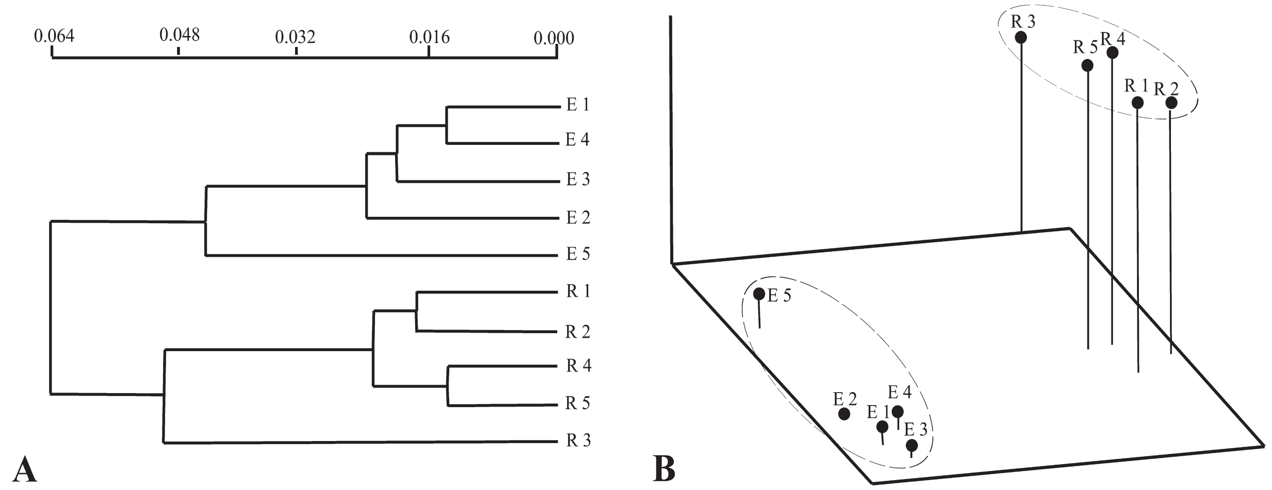

FIG. 6. – Cluster (A) and MDS-3D (B) based on the average of the lengths of cnidae common to *Balanophyllia europaea* (E1 to E5) and *Balanophyllia regia* (R1 to R5); see Figure 2 and Table 1 for locations and collecting data.

and *B. regia*. In each table, all sampling stations and individuals examined in this study are considered.

Holotrich 2	Holotrich 3	Mic. *p*-mastigophore 1	Mic. *p*-mastigophore 2	Mic. *p*-mastigophore 3
	90.47±8.19 x 19.77±1.42 (65.7-112 x 15.2-24.2) (++)	18.57±1.81 x 5.33±0.84 (14.1-24.2 x 3.5-7) (++)		
39.21±4.03 x 5.67±0.55 (28.3-48.5 x 4-7) (-)				35.97±3.74 x 4.84±0.46 (26.3-45.5 x 4-6) (+++)
34.68±4.37 x 6.36±0.69 (24.2-49.5 x 5-9) (++)				
30.91±3.16 x 6.79±0.7 (19.2-41.4 x 5-9) (+)			27.83±2.77 x 6.34±0.76 (21.2-37.4 x 5-8) (+++)	
	91.15±6.7 x 19.88±2.03 (107-64.6 x 28.3 x 15.2) (++)			
	76.09±7.95 x 20.69±1.51 (44.4-95 x 16.2-25.3) (++)			
37.45±3.96 x 6.62±0.8 (26.3-47.5 x 4.5-8.5) (+)				33.47±3.68 x 5.32±0.67 (25.3-43.4 x 3-7) (++)
32.99±2.8 x 7.3±0.91 (26.3-40.4 x 5-9) (++)				
29.62±2.63 x 7.02±0.77 (23.2-36.4 x 4.5-9) (+)			27.33±2.8 x 7.09±0.8 (20.2-39.4 x 5.5-9.6) (+++)	
	73.31±5.9 x 19.76±2.4 (55.6-87.9 x 14.1-23.7) (+)			

few later papers dealing with the taxonomic value of the cnidome in scleractinians (Carlgren, 1940, 1945; Pires, 1997). Thus, many of the following comments will also refer to the papers discussing this aspect in “soft” hexacorallians.

Our study shows that the cnidome of *Balanophyllia europaea* and *B. regia* is constant in composition and size range throughout a wide geographic area. The cnidome is one more distinguishing character of these species. Intraspecific variability from one station to the other remains lower than differences between any pair of samples of the two species compared, apart from the qualitative difference (one type more in *Balanophyllia europaea*).

According to Fautin (1988), each taxon is expect to have nematocysts of a characteristic size range and/or distribution. This premise is essential for admitting the cnidome as a valid taxonomic character in scleractinians, but it should take into account intraspecific variability that may be expressed at geographical, ontogenetic or ecological levels (e.g. Williams, 1998), as well as the spatial distribution of the cnidae in different parts of the polyp, since this may not be homogeneous (Ardelean, 2003).

Qualitative differences at a generic level in scleractinian were already observed by Pires and Pitombo (1992) Brazilian Mussidae (four species, three of them congeneric). All three species of the genus *Mussismilia* had two size categories of p-rabdoids D (microbasic *p*-mastigophore in our nomenclature) in the mesenterial filaments, whereas the species of *Scolymia* had only a single category. Specific differences between *Mussismilia* species were expressed mainly at average level, with an overlapping of SD and size range of the cnidae categories. More measurements and additional statistical analyses would probably confirm these trends. Subsequently, Pires (1997) suggested including the cnidome as an additional tool in coral and systematic taxonomy.

As for sea anemones, William (2000) argued that only the lack of overlap of maximum standard range of cnida length reliably indicates that samples are not conspecific. However, partial or complete overlap of cnida size extremes does not necessarily indicate that specimens are conspecific; other taxonomic characters must also be considered.

The present study has shown that cnida characters can be used to separate congeneric species, both from a qualitative and quantitative point of view.

Basitrichs 1 (scapus and columella) and microbasic *p*-mastigophores 1 (scapus) were present in *B. europaea* only. The average value including its SD is different in both *Balanophyllia* species (see Tables 2, 3, and Figures 4, 5). This shows that widely separate populations in two congeneric species maintain (with an acceptable range of intraspecific variability) a stable set of cnidome characteristics suitable for distinguishing the species.

The investigation done here should be extended to ontogenetic stages of the two species, especially in more isolated so probably genetically more homogeneous populations. It would further be of great interest to investigate more widely the scleractinian cnidome on the generic and higher category levels. Detailed knowledge of the cnidome could well help to reorganise the conventional classification of the scleractinian, so far based on the skeleton only.

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