The morphology of *Ralfsia expansa* (J. Agardh) J. Agardh (Ralfsiaceae, Phaeophyta) from Veracruz, Mexico

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Abstract – The holotype specimen of *Ralfsia expansa* is examined, and a description including the characteristics that are presently used to distinguish the species of the genus is provided. Considering that the type specimen is sterile and that different interpretations of the species exist, its reproductive structures are described based on specimens obtained from the type locality, in Veracruz, Mexico. The observations show that the unangia of the species are characteristically borne on a one-celled. This feature distinguishes the species from the very near *R. hancockii* which has multicelled stalks. *Ralfsia expansa* can be distinguished from *R. fungiformis*, *R. verrucosa*, *R. hancockii*, *R. hesperia*, *R. integra*, *R. longicellularis* and *R. huanghaiensis* by a combination of reproductive features, the presence of a clearly defined cortical layer, and its growth form. *Ralfsia pacifica* does not have a cortical layer and a unangial stalk and is not distinct from *R. verrucosa*. *R. expansa* has been reported from the tropical and subtropical Atlantic, the Mediterranean Sea, and the coasts of India.

Taxonomy / distribution / reproductive structures / circumscription / Ralfsia expansa / R. pacifica / R. hesperia / R. integra / R. fungiformis / R. verrucosa / R. hancockii / R. longicellularis / R. huanghaiensis.

Résumé – Morphologie de Ralfsia expansa (J. Agardh) J. Agardh (Ralfsiaceae, Phaeophyta) from Veracruz, Mexico. L'holotype de Ralfsia expansa a été examiné et décrit, en particulier pour ce qui concerne les critères actuels qui permettent de distinguer les espèces du genre. Puisque le spécimen type est stérile et que différentes interprétations de l'espèce existent, ses structures de la reproduction ont été décrites sur des spécimens récoltés dans la localité type, Veracruz, Mexico. Les observations montrent que les sporocystes uniloculaires de l'espèce se forment de façon caractéristique sur une cellule unique. Ceci distingue l'espèce de R. hancockii très proche dont les celules-pied des sporocystes sont multicellulaires. Ralfsia expansa peut se distinguer de R. fungiformis, R. verrucosa, R. hancockii, R. hesperia, R. integra, R. longicellularis et R. huanghaiensis par une combinaison de caractères liés à la reproduction, la présence d'une couche corticale clairement définie et sa forme de croissance. Ralfsia pacifica n'a pas de couche corticale ni sporocystes pourvus d'un pied et n'est pas distinct de R. verrucosa. R. expansa est répertorié dans l'Atlantique tropical et subtropical, dans la Méditerranée et sur les côtes de l'Inde.

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INTRODUCTION

Ralfsia Berkelev in Smith & Sowerby (1843: 2866) includes approximately 20 species of brown crustose algae that in habit are initially more-or-less orbicular in outline and later become irregular or lobed at the margins. Anatomically, they are two-layered with perpendicularly disposed filaments: prostrate and erect filaments, the erect arising from the prostrate, each cell with a laminar parietal chloroplast without pyrenoids. The erect filaments are loosely to tightly adherent throughout their entire length, depending on the species. Ralfsia has been subdivided into two subgenera: Eu-Ralfsia Batters and Stragularia (Strömfelt) Batters (Batters 1890, 1902; De Toni, 1895). The former includes those species with tightly adherent filaments, which are arched, ascending from the prostrate filaments and with definite prominent sori. Stragularia includes species with mainly loose, erect filaments perpendicular to the prostrate filaments and sori in irregular patches or forming a continuous layer. However, according to Kjellman (1893), Weber van Bosse (1913), Hamel (1939), Wynne (1969) and Fletcher (1987), Stragularia Strömfelt (1886) is an independent genus and it must be reviewed. The species of Ralfsia sensu Eu-Ralfsia are distinguished by the presence of a cortical layer with small cells and a medulla with larger cells, a stalked unangium and the number of cells in the stalk. The terms unangia and plurangia are used to meaning unilocular or plurilocular reproductive structures, the nature of whose reproductive cells (i.e. gametes or spores) is unknown.

Ralfsia expansa (J. Agardh) J. Agardh was described (1847: as Myrionema (?) expansum, 1848) from sterile specimens collected by Liebmann from an unspecified area on the coast of Veracruz, Mexico in 1817. The description is very rudimentary and not diagnostic. Børgesen (1912) described specimens from the Danish West Indies that he found quite similar to the type of R. expansa. His study has been the basis for recognizing the species directly or indirectly through other authors who cite it (cf. Børgesen, 1912 with Børgesen, 1914; Weber-van Bosse, 1913; Joly, 1965; Earle, 1969; Taylor, 1960; Schnetter, 1976; Lawson & John, 1982). In their revision of the Ralfsiales (Tanaka & Chihara, 1980a,b,c, 1981a,b,c), Tanaka & Chihara (1980b) described the reproductive structures of R. expansa collected from the Japanese islands. Their description differed from that of Børgesen (1912), and this has generated new interpretations of the species. However, León-Alvarez & González-González (2003) are of the opinion that the unangial specimens with multicelled stalks described by Tanaka & Chihara correspond to Ralfsia hancockii Dawson (1944). The latter was first described from the Gulf of California and is frequently collected in the Mexican Tropical Pacific (León-Alvarez & González-González, 1995). As the holotype of R. expansa is sterile, the diagnostic value of its reproductive characteristics is debatable. For this reason, this paper presents the first record and description of the unangial reproductive structures of the species based on topotype material. A description of the holotype specimen of Ralfsia expansa is also provided.

MATERIAL AND METHODS

The locality of Morro de la Mancha was visited during the months of August 1991, July and October 2001, February 2002 and 2003 and June 2004. This is a rocky beach where the Centro de Investigaciones Costeras La Mancha, of the

Instituto de Ecología A.C. of Jalapa, Veracruz is located at 96°22' W and 19°30' N. Fragments of rock with specimens of *R. expansa* were removed from the mid to high intertidal from an exposed rocky platform. The samples were observed under a stereoscopic microscope, three fragments of different specimens were obtained, and radial-vertical sections were prepared by hand, stained with malachite green, and mounted with glycerinated gelatin (González-González & Novelo-Maldonado, 1986). One to three slides were prepared for each sample, which are deposited in the algal collection of the Herbario de la Facultad de Ciencias, of the Universidad Nacional Autónoma de México (FCME) under the following registry numbers: slide 244 (17/ago/1991), GM-284 (1/jul/2001), GM-285 (5/oct/2001), GM-286 (14/feb/2002), GM-289 (14/feb/2003), GM-290 (14/feb/2003), GM-291 (14/feb/2003) and GM-389 (11/jul/2004).

Small pieces of the herbarium specimens were detached using a stere-omicroscope and rehydrated in a detergent solution for 15 min. Radial-vertical sections were prepared by hand, stained with methylene blue, and mounted with glycerinated gelatin. The following specimens were examined: the holotype of *Ralfsia expansa* (J. Agardh) J. Agardh (Fig. 1) (internally labeled as *Myrionema expansum* J. Agardh, A681, undated) from the Botanical Museum and Herbarium of Copenhagen (C), one specimen of *R. expansa* of the Herbarium of the Escuela Nacional de Ciencias Biológicas of the Instituto Politécnico Nacional (ENCB4257, 9/Nov/1976) from Punta Limón, Veracruz, Mexico and the holotype of *Ralfsia integra* Hollenberg (US61155) from the National Herbarium of the Smithsonian Institution, Washington DC.

Specimens were described in accordance with criteria used by the authors Areschoug (1843), J. Agardh (1848), Børgesen (1912), Setchell & Gardner (1924, 1925), Hollenberg (1969), and Tanaka & Chihara (1980a,b,c, 1981a,b,c). Microscopic observations were made under a ZETOPAN microscope. Each characteristic was measured 10 times throughout the length of the specimen.

RESULTS

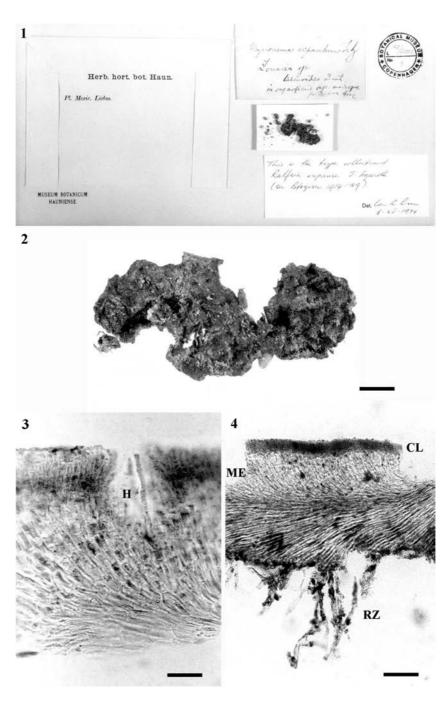
Type specimen

Ralfsia expansa (J. Agardh) J. Agardh 1848: 63 (=Myrionema (?) expansum J. Agardh 1847: 7).

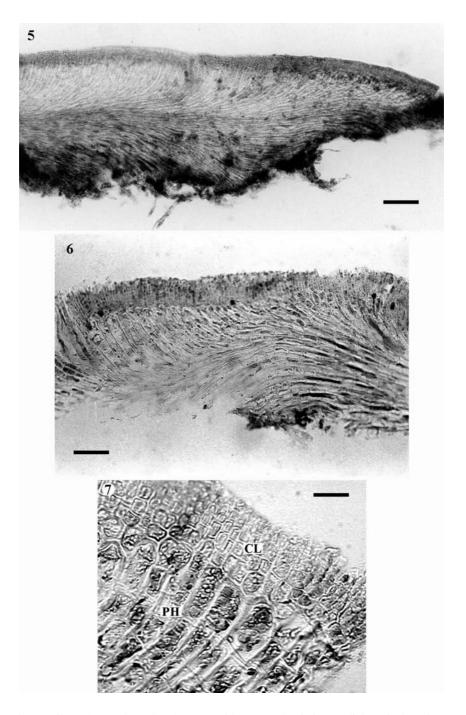
Holotype. Recorded under the basionym *Myrionema expansa* in the type database of the Botanical Museum and Herbarium, Copenhagen (C), Number A681 (internally labelled as Botanical Museum Copenhagen L 78/2002, No. 7) (Fig. 1), collected by Liebman in Veracruz, Mexico. Undated.

Orbicular to irregular crustose algae, 1.5-2.5 cm in diameter, dark brown to black when moist and brown when dry, with radial growth lines and prominent margins without lobes. Thallus surface rugose (Fig. 2), with a smooth texture that does not disintegrate when rubbed between the fingers. Thickness is 449-649 μ m (without rhizoids).

Thallus with single hyaline hairs in spheroid cryptostomata or in pits or clefts, arising at half thickness from the thallus surface in the medullary filaments (Fig. 3). Rhizoids are irregularly distributed over the lower surface of the thallus (Fig. 4). Ascocysts are absent. In radial-vertical sections, filaments grow bilaterally throughout the crust with an evident central axis (Fig. 5). Medullary filaments,



Figs 1-4. **1.** Holotype specimen of *Ralfsia expansa* in the Botany Museum of Copenhagen (A681). **2.** Rough texture type specimen of *R. expansa*. Bar = 0.46 cm. **3.** Radial-vertical section with hyaline hairs (H) in spheroid cryptostomata. Bar = 37 μ m. **4.** Radial-vertical section with rhizoids (RZ), medulla (ME) and cortical layer (CL). Bar = 130 μ m.



Figs 5-7. **5.** Bilateral growth of the filaments with a central axis in a radial-vertical section. Bar = $130 \mu m$. **6.** Upper part of a longitudinal section with branched medullary filaments curving and rising. Bar = $75 \mu m$. **7.** Subcortical cells with physodes (PH) and cortical layer (CL). Bar = $17 \mu m$.

tightly united throughout their entire length, arising from prostrate filaments that are irregularly arranged (*i.e.* not in layers). Prostrate filaments consisting of cylindrical to irregularly shaped cells, which are united by a transverse like notch septum. Medullary filaments curve upward as a result of repeated ramification, become thinner or equal towards the apex (Fig. 6), branching about eight times. A gelatinous matrix does not surround them. Erect filaments consist of irregular to cylindrical cells in the basal part, 17-37 μ m in length \times 12-15 μ m in diameter and l/d 1.4-2.5. They have botuliform to cylindrical, or irregular to subspherical subcortical cells, with thin (less than a third of the diameter of the cell) walls, 17-30 μ m in length \times 12-13 μ m in diameter and l/d 1.1-2.3, and with abundant physodes (like hyaline discoid granules) (Fig. 7). The cortical layer is 5-6 cells thick and is clearly morphologically differentiated from the medullary cells (Fig. 7). Cortical cells are mainly barrel-shaped and the apical cells are dome-shaped, 8-13 \times 5-8 μ m and l/d 1.5-2, with a parietal laminar chloroplast. Pyrenoids are not evident. The specimen is sterile.

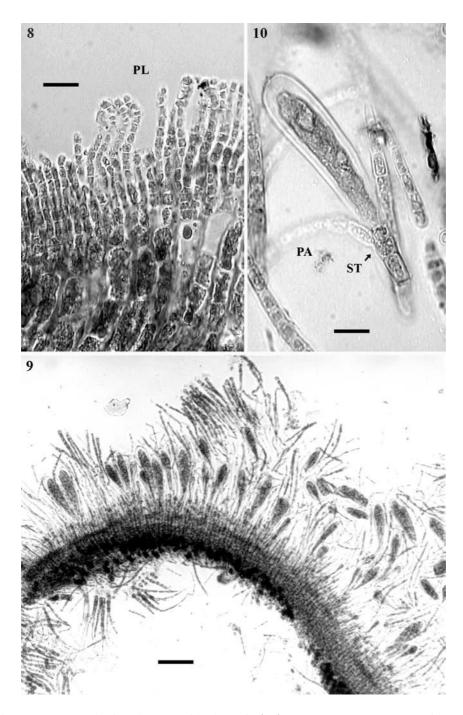
Specimens from Veracruz

Orbicular to irregular crustose algae, 1-5 cm in diameter, dark brown to black when moist and light brown when dry, sometimes with radial growth lines and prominent margins without lobulations. Thallus surface frequently rugose, of a smooth texture which does not disintegrate when rubbed between the fingers. The thickness of the vegetative thallus is 180-450 μ m (without rhizoids), and 315 - 450 μ m in the reproductive parts. In a longitudinal radial view the filaments have bilateral symmetry mainly in areas that coincide with irregularities of the substrate, although in other regions the filaments grow unilaterally. Basal cells of the medullary filaments are 24-52 μ m in length \times 10-18 μ m in diameter and length/diameter (I/d) is 1.6-4.2. The cortical layer is 3-5 cells thick, with cubic to cylindrical cells, 3-6 μ m \times 4-6 μ m and I/d 0.7-1.2.

Plurangia were found in the specimen from Punta Limón. Plurangia are located in sori that are distributed irregularly throughout the thallus and are covered by a gelatinous layer. They originate terminally on reproductive erect medullary filaments and are not associated with paraphyses (Fig. 8). Generally, 1-2 plurangia form per filament. The plurangia are cylindrical, 25-88 $\mu m \times 4$ -8 μm , and consist of a series of cylindrical cells and one terminal sterile dome-shaped cell, 6-8 $\mu m \times 4$ -6 μm and 1/d 1.2-1.7.

Unangia were found in one specimen from Morro de la Mancha. Unangia are present in sori which are scattered sparsely on the thallus. They are surrounded by slender claviform paraphyses that are differentiated morphologically from the reproductive filaments (Fig. 9). Single unangia occur at the terminal end of barrel-shaped unicellular stalks or uncommonly at the basis of the paraphyses. These are ovoid when young, claviform or sometimes pyriform when mature, 72-112 \times 25-32 μm . Paraphyses are 155 μm in length and contain 13-15 cells: basal cylindrical cells 10×7 μm and length/diameter ratio of 1.4, and obovoid subapical cells $7\text{-}8\times6\text{-}7$ μm and l/d of 1.1.

Ralfsia expansa was collected in a vegetative state in August 1991, July and October 2001, in February 2002 and in June 2004 from the rocky seaboard of Morro de la Mancha, Veracruz, although unangia were found only in February 2003 (FCME-GM-289). The alga grew forming 3-5 cm diameter orbicular dots or extensive continuous plots, on the upper crest or prominences of the rocks along the mid to high intertidal fringe, exposed to strong wave shock, where the water is quickly drained, remaining exposed to solar irradiation and drying out completely during the low tide.



Figs 8-10. **8.** Reproductive filaments with plurangia (PL). Bar = 17 μ m. **9.** Upper section of a squashed sorus with unangia and paraphyses. Bar = 70 μ m. **10.** Squashed slide showing one cell stalked (ST) unangium with paraphysis (PA) arising behind it (out of focus). Bar = 19 μ m.

DISCUSSION

The specimens from Punta Limón and from Morro de la Mancha agree well with the type specimen, however some differences were observed: the thickness of the vegetative thallus and of the cortical cells is less than in the holotype. We consider these differences a result of the development of the crusts with age, because the older cells (*i.e.* basal and near to basal layers) are of similar size in both the specimens from La Mancha and in the type specimen. However, we must study the species under culture and look for thicker crusts throughout a greater gradient of environmental conditions so as to include a bigger range of variation of the species.

In Børgesen's study of *Ralfsia expansa* from the Danish West Indies (Børgesen, 1912) he observed that "often the leaf is more or less bilateral", and is similar to a form of *R. verrucosa* from the English Channel depicted in Reinke (1889a, p. 48, fig. c, as *R. verrucosa* Le Jolis). Børgesen even suggested the possibility that *R. expansa* could be a form of *R. verrucosa* Areschoug. Symmetry varies in the same specimen and between different specimens from Veracruz, confirming the opinion of León-Alvarez & González-González (2003) that the intraspecific variation undermines the diagnostic value of the character. However, Børgesen did not notice the presence of a multistratose cortical layer which is not present in *R. verrucosa* (vide Reinke, 1889b) and has been used as an important feature to distinguish species of *Ralfsia* (Tanaka & Chihara, 1980a,b,c, 1981a,b,c).

Reproductive structures have frequently been used as diagnostic characteristics of the species. When Børgesen (1912) described them, he noted that the "unilocular sporangia" of R. expansa almost always had a unicellular stalk, and only rarely were they found without it. Børgesen used this characteristic together with the size of the unangia to distinguish R. expansa from R. verrucosa. Tanaka and Chihara (1980a) assigned specimens, collected in the warmer seas of Japan, to R. expansa. These were characterised by unangia subtended by stalks 3-6 cells long and they considered the difference with respect to Børgesen's unicellular stalks "as a result of differences in strains" sic. Nevertheless, in other studies that have illustrated or described in detail the reproductive structures of R. expansa (e.g. Schnetter, 1976; Balakrishnan & Kinkar, 1981; Széchy-Menezes de, 1986; Sartoni & Boddi, 1989), the unangia are always borne on unicellular stalks. In some reports it has been indicated that stalks may be absent on rare occasions, but they have never been reported to be multicellular. The constancy of these observations on specimens originating from geographical areas as distant as the Caribbean coast of Colombia, the seaboard of Rio do Janeiro, Brazil, the Island Alboran in the Mediterranean, and the coasts of India suggests that this feature is characteristic of the species, and this is confirmed in the present study based on topotype

According to the description of the specimens of *R. expansa* from Veracruz, this species can be distinguished from other species of the genus *Ralfsia* sensu *Euralfsia* (Batters 1890) by considering both its reproductive and vegetative characteristics. The most similar species to *R. expansa* with unicellular stalks are *R. hesperia* Setchell & Gardner, *R. integra* Hollenberg and *R. huanghaiensis* Xiyi & Junfeng (Tab. 1). *Ralfsia expansa* differs from the first species in that its reproductive characteristics are smaller, from the second by presenting a multistratose cortical layer (according to observations of the Holotype US61155 of *R. integra*), and from *R. huanghaiensis* because the thallus does not form trichotomous branches (Xiyi & Junfeng, 1993). According to the observations on the lectotype

Species	Unangia Length- diameter (µm)	Stalks Cell number	Paraphyses		Plurangia	
			Length (μm)	Cell number	Length- diameter (µm)	Layers
R. expansa (1,2)	75-120 × 25-35	1	100-190(220)	8-14	25-87 × 4-7	1
R. fungiformis (Gunnerus) Stechell & Gardner (3)	up to 115 × 22	sessile	140	5-6	up to 180 × 11	1
R. hancockii (4,5)	(62)90-110 × 20-30(42)	(2)3-6(7)	150-175	10-13(18)	unknown	
R. hesperia (6, 7)	120-140(180) × 28-34	0-1	290-360	9-12	unknown	
R. integra (7)	60-100(140) 1 × 18-25	mainly sessile -1 (growing unangia)	130-180 (200)	8-12	unknown	
R. longicellularis Perestenko (8)	65-92 × 22.5-31	multicellular	190-210	10-13	unknown	
R. verrucosa (9, 10)	50-60(72) × 20-25	sessile	70-120	6-10	$40-50 \times 5$	1
R. huanghaiensis (11)	100-110 × 24-28	1	200-208	8-10	+/-50	1

Table 1. Reproductive characteristics of the species of Ralfsia sensu Euralfsia.

References: 1 = This study, 2 = Børgesen (1912), 3 = Edelstein *et. al.* 1968, 4 = Dawson 1944, 5 = León-Alvarez & González-González (2003), 6 = Setchell & Gardner 1924, 7 = Hollenberg 1969, 8 = Perestenko 1980, 9 = Reinke 1889b, 10 = Tanaka & Chihara, 1980a, 11 = Xiyi & Junfeng 1993.

of *R. pacifica* Hollenberg (US611158) made by León-Alvarez & González-González (2003), this species does not have a cortical layer and a unangial stalk and consequently is almost identical with *R. verrucosa*. These observations agree with Womersley's (1987: 72) opinion that *R. pacifica* is not distinct from *R. verrucosa*.

Ralfsia expansa is the only species of the genus registered by Wynne (1998) in the checklist of benthic marine algae of the tropical and subtropical Western Atlantic. Its distribution covers the Gulf of Mexico and the tropical and subtropical Atlantic (J. Agardh, 1847, 1848; Taylor, 1928, 1942; Earle, 1969; Taylor, 1960; Garza-Barrientos, 1975; Schnetter, 1976; Huerta-Múzquiz & Garza-Barrientos, 1980; Sánchez-Rodríguez, 1980; Huerta-Múzquiz et al., 1987; Aguilar-Rosas et al., 1998; Díaz-Martín & Espinoza-Avalos, 2000; vide Lawson & John, 1982 for references in Africa). The species has also been reported in the Mexican Tropical Pacific (MTP) (Chávez, 1972; León et al., 1993; Serviere et al., 1998). Nevertheless, León-Alvarez & González-González (2003) noted that the records of R. expansa in the MTP correspond to R. hancockii Dawson. We have compared the morphological descriptions of R. expansa by Sartoni & Boddi (1989) and Balakrishnan & Kinkar (1981) from geographical areas as distant as the Mediterranean and the coasts of India, and both fit well with our description of the specimens from Veracruz and the type species. Notwithstanding our morphological circumscription of the species, there is no reason to consider cryptic diversity that the molecular studies could prove, and we believe that the species has a worldwide distribution that is mainly restricted to the tropical and subtropical fringes. This species has not been found in the tropical Pacific where the closely related *R. hancockii* is common (León-Alvarez & González-González, 1995), from which it could have separate (and change little), when the Tehuantepec isthmus closed during the Tertiary period 3.5-4 million years ago (Tamayo, 1949, see León-Alvarez & González-González, 2003).

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