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Anatomical characteristics and reproductive structures of *Kallymenia lacerata* (Kallymeniaceae, Rhodophyta) from the Mediterranean Sea

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Résumé — Caractéristiques anatomiques et structure de la reproduction de *Kallymenia lacerata* (Kallymeniaceae, Rhodophyta) de la Méditerranée. Plusieurs caractéristiques végétatives et reproductives de l'algue rouge *Kallymenia lacerata* de Méditerranée sont décrites pour la première fois. *K. lacerata* est caractérisée par la combinaison de caractères suivante : des frondes adultes laciniées, des cellules corticales externes disposées en rosette autour des cellules qui sont au dessous, des cellules médullaires étoilées avec un corps cellulaire allongé et des prolongements disposés distalement, des spermatocystes groupés en sores, des systèmes carpogoniaux composés d'une cellule support portant des rameaux carpogoniaux et des cellules subsidiaires où le reste du rameau carpogonial (la cellule hypogyne et le carpogone) n'est pas développé, et des tétrasporocystes cruciés dispersés sur la surface de la lame. *K. lacerata* est comparée à l'espèce type, *K. reniformis*, aux autres espèces du genre de l'Ouest de la Méditerranée et au genre *Thamnophyllis*.

***Kallymenia lacerata* / *Kallymenia*ceae / Gigartinales / morphologie végétative / reproduction / Rhodophyta / taxinomie**

Abstract — Several vegetative and reproductive characters of the Mediterranean red alga *Kallymenia lacerata* are described here for the first time. *K. lacerata* is characterized by the following combination of features: laciniate adult blades, outer cortical cells spreading and forming rosettes around cells of the cortical layer underneath, elongated stellate medullary cells with distal arms, spermatangia grouped in sori, carpogonial branch systems consisting of supporting cells bearing both three-celled carpogonial branches and subsidiary cells that lack the hypogynous cell and the carpogonium, and cruciately divided tetrasporangia scattered over the thallus surface. *K. lacerata* is compared with the type species, *K. reniformis*, with other species of *Kallymenia* from the Western Mediterranean Sea, and with the genus *Thamnophyllis*.

***Kallymenia lacerata* / *Kallymenia*ceae / Gigartinales / reproduction / Rhodophyta / taxonomy / vegetative morphology**

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INTRODUCTION

The genus *Kallymenia* J. Agardh (Gigartinales, Rhodophyta), based on the type species *K. reniformis* (Turner) J. Agardh (1842, p. 99), is characterized vegetatively by *i)* a cortex composed of various layers of cells diminishing in size outwardly, and *ii)* an essentially filamentous medulla with some interspersed ganglionic or stellate cells, and reproductively by *iii)* spermatangia either grouped in sori or scattered over the thallus surface, *iv)* a non-procarpic female reproductive apparatus, *v)* mono- or polycarpogonial branch systems composed of a rounded or lobed supporting cell that gives rise to one or several 3-celled carpogonial branches and some subsidiary cells, *vi)* fusion cells formed after fertilization, involving the supporting cell and subsidiary cells, *vii)* auxiliary cell systems composed of a rounded or ovoid supporting cell that supports several subsidiary cells, *viii)* long non-septate connecting filaments issuing from fusion cells, *ix)* carposporophytes consisting of numerous carposporangia intermixed with secondary vegetative filaments within the medulla, and *x)* cruciately, zonately or irregularly divided tetrasporangia scattered over the thallus surface within the outer cortex (Norris, 1957; Codomier, 1968, 1971, 1972; Hommersand & Ott, 1970; Womersley & Norris, 1971; Womersley, 1994; Vergés, 2001).

Kallymenia currently includes six species in the Mediterranean Sea: *K. reniformis, K. feldmannii* Codomier (1971), *K. lacerata* Feldmann (1942), *K. requienii* (J. Agardh) J. Agardh (1842), *K. patens* (J. Agardh) Codomier *ex* P.G. Parkinson (1980) and *K. spathulata* (J. Agardh) Codomier *ex* P.G. Parkinson (1980) (Codomier, 1968, 1971, 1972; Vergés, 2001). Male and female reproductive structures are fully known in *K. reniformis* and *K. feldmannii,* partially known in *K. requienii,* and completely unknown in *K. patens* and *K. spathulata* (Vergés, 2001). *K. lacerata*, a species originally described from a fertile female gametophyte collected by J. Feldmann in Banc de Matifou (also known as Bordj-El-Bahri), Algeria (Feldmann, 1942), is characterized by *i)* a simple or lacerate blade, *ii)* a cortex composed of four layers of cells diminishing in size outwardly, *iii)* a filamentous medulla with some interspersed stellate cells, *iv)* carposporophytes consisting of numerous carposporangia, and *v)* scattered, cruciately divided tetrasporangia (Feldmann, 1942; Codomier, 1968, 1971, 1972; Huvé & Passelaigue, 1970; Vergés, 2001). The male and female reproductive structures and postfertilization stages of this species are unknown.

In the present paper, the study of numerous specimens of *K. lacerata* from the Mediterranean coast of Spain and Corsica (France) has allowed us to fully describe its vegetative morphology and male and female reproductive structures. These features are compared with those of the type species, with the other species of *Kallymenia* living in the same area, and with the related genus *Thamnophyllis*.

MATERIALS AND METHODS

This study is based on the examination of specimens collected by SCUBA divers between January 1996 and September 2004 on the coasts of the western Mediterranean (Spain and France). Specimens were collected throughout the year

on sublittoral rock at depths ranging from 10 to 50 m, but, due to the strong seasonality of the species, sampling was intensified in spring and summer. Plants were fixed and preserved in a solution of 4% formalin in seawater. Sections were made with a razor blade and were subsequently stained in an acidified 1% aniline-blue/distilled water solution and mounted permanently in 50% Karo® corn syrup. Drawings were made using a Labophot 2 Nikon (Nikon, Tokyo, Japan) microscope with a camera lucida attachment. Photographs of the habits were taken with a *Pentax Programa* camera (Pentax, Golden, CO, USA) and light microscope photographs were taken with a *Nikon F-601M* camera attached to a Labophot 2 Nikon microscope and a Spot Insight digital camera (Diagnostic Instruments, Sterling Heights, MI, USA) attached to an Axioskop 2 plus Zeiss microscope (Zeiss, Berlin, Germany).

Voucher specimens and slides have been deposited in the Herbarium of the University of Girona, Spain, algae section (HGI-A).

Representative specimens examined:

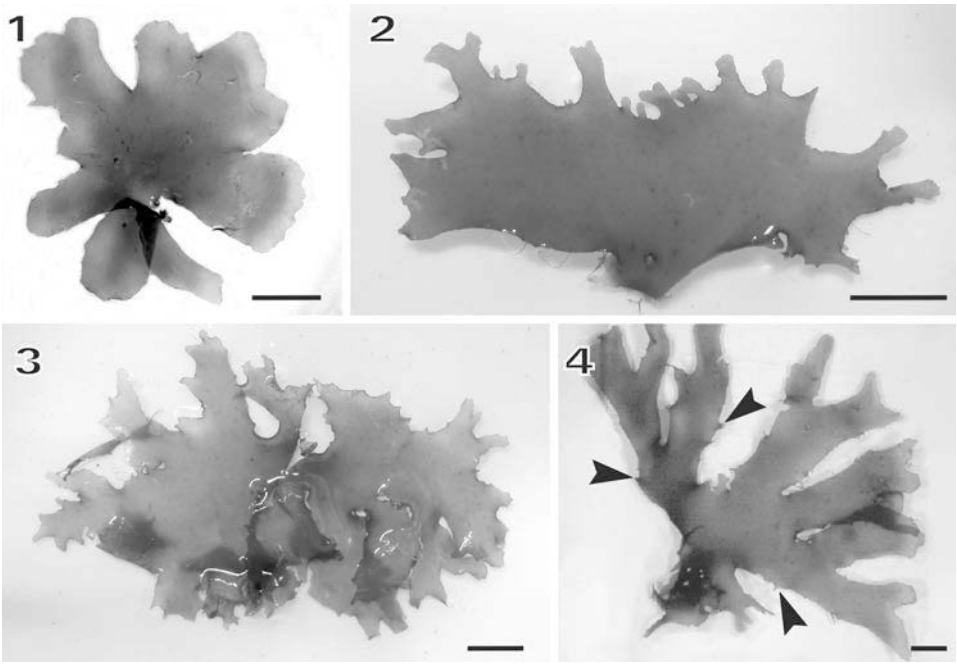
***SPAIN*: CATALONIA**. PALAMÓS - Formigues Islands, collected by (coll.) *C. Rodríguez-Prieto*: 30 August 1998, 38 m deep, HGI-A 4040 sterile; 6 December 1998, 42 m deep, HGI-A 4041 ♀; 1 August 1999, 30 m deep, HGI-A 4775 ⚥, 4777 ♀, 4779 ⚥; 11 September 2000, 43 m deep, HGI-A 5238 ♂; 12 August 2001, 38 m deep, HGI-A 5258 ♂, 5261 ♂; 29 September 2002, 45 m deep, HGI-A 5685 ♂; 22 August 2004, 35 m deep, HGI-A 6521 sterile; 19 September 2004, 35 m deep, HGI-A 6522 sterile. LLAFRANCH – coll. *C. Rodríguez-Prieto*, 25 July 1999, 45 m deep, HGI-A 4776 ♂, 4784 ♂. **CABRERA (Balearic Islands)** – COVA BLAVA - coll. *C. Rodríguez-Prieto*, 23 May 1996, 10 m deep, HGI-A 4000 sterile; CAP FALCÓ, coll. *C. Rodríguez-Prieto*, 24 May 1996, 50 m deep, HGI-A 4034 sterile; 29 May 1996, 50 m deep, HGI-A 4009 sterile; ELS ESTELLS, coll. *C. Rodríguez-Prieto*, 25 May 1996, 50 m deep, HGI-A 4007 sterile, 4008 sterile; I. DE L'IMPERIAL – coll. *C. Rodríguez-Prieto*, 30 May 1996, 50 m deep, HGI-A 4004 sterile, 4005 sterile. – coll. *E. Ballesteros*, 20 May 2004, 62-67 m deep, HGI-A 6361 sterile, 6362 sterile, 6366 sterile. **COLUMBRETS ISLANDS**: COLUMBRET GRAN – coll. *E. Ballesteros*, 20 June 1996, 42 m deep, HGI-A 4002 sterile; PIEDRA JOAQUÍN – coll. *E. Ballesteros*, June 1996, 55 m deep, HGI-A 4003 sterile, 4006 sterile; MANCO LIBRE – coll. *C. Rodríguez-Prieto and N. Sánchez,* 15 September 2002, 40 m deep, HGI-A 5656 ♀, 5657 ♀, 5658 ♀, 5659 ♀, 5660 ♀.

***FRANCE*: MARSEILLE.** NIOLON – coll. *P. and H. Huvé*, 23 August 1967, 23 m deep, H 2902 ⊕. **CORSICA**. PALAZZINO – coll. *E. Ballesteros*: 1 October 2000, 30 m deep, HGI-A 4878 ♀; 1 October 2001, 30 m deep, HGI-A 5297 ♀, 5298 ♀, 5299 ♀, 5300 ♀, 5301 ♀, 5302 ♀, 5303 ♀.

RESULTS

***Kallymenia lacerata* Feldmann 1942: 10** (Figs 1-21).

Type locality: Banc de Matifou, Algeria, 20 October 1938, 15-35 m, herbarium J. Feldmann nº 4877.



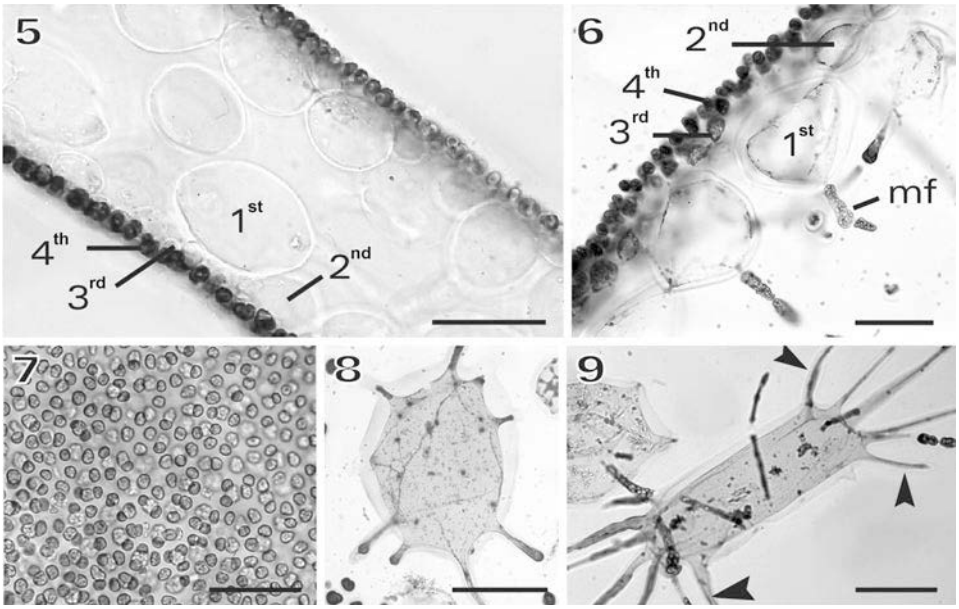
Figs 1-4**.** Morphology of *Kallymenia lacerata.* **1-2.** Habit of a young individual (HGI-A 6362). **3-4.** Habit of adult individuals (HGI-A 6521, 6522, 4777). Arrowheads indicate dentate margins. Scale bars = 1 cm.

Distribution*:* Mediterranean Sea. Widely distributed in the western Mediterranean and found only once in the eastern Mediterranean (Rodríguez-Prieto & Vergés, 2001).

Habitat and seasonality: *Kallymenia lacerata* is annual, occurring in the circalittoral, on coralligenous bottoms and in the maërl usually at depths of more than 30-40 m (Rodríguez-Prieto & Vergés, 2001). Specimens of *K. lacerata* were collected from spring until early autumn, when storms destroy the fronds, although one individual was found in December 1998 (HGI-A 4041). Smaller individuals were found from April to June and were sterile. Bigger and occasionally fertile specimens were found from late May to October.

Habit: Fronds are up to 9 cm long, 14 cm wide and 170-280 μm thick, flattened, sessile, rose to carmine in colour, and arise from a small discoid holdfast. Thalli are initially simple or lobed and become laciniate in adult specimens (Figs 1-4), with smooth or occasionally dentate margins (Fig. 4). Fronds are partly overlapping and occasionally anastomose, with delicately membranous and slippery blades.

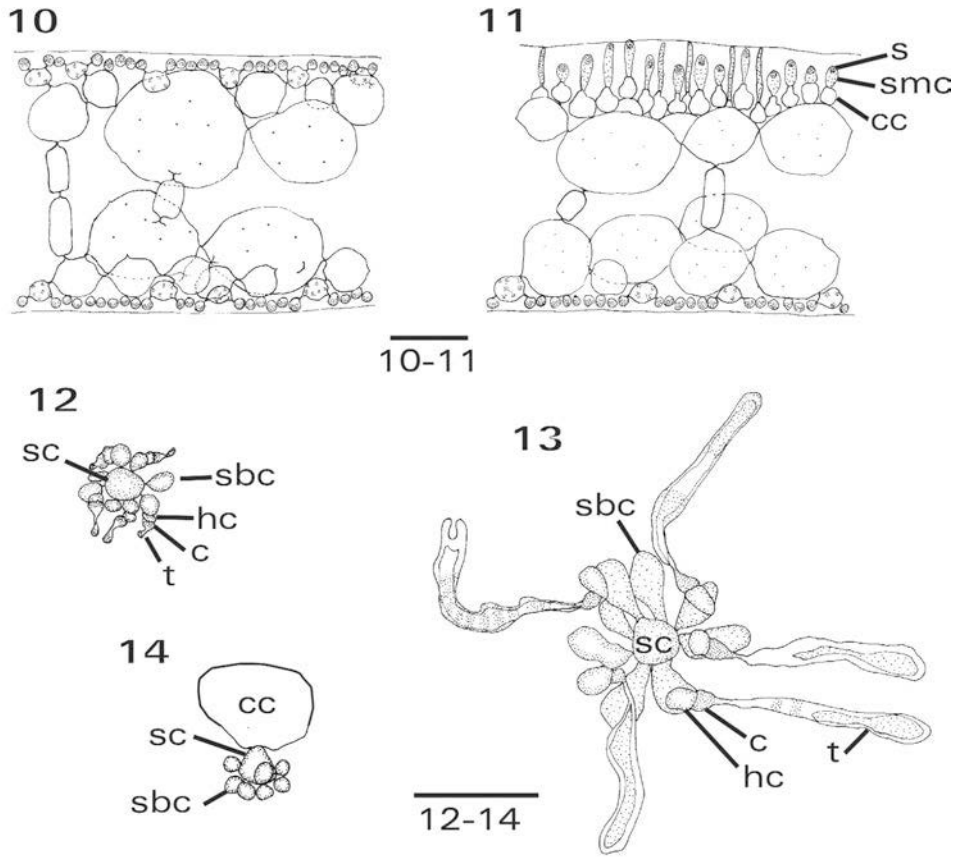
Vegetative structure: The structure is multiaxial, with a cortex composed of four layers of cells decreasing progressively in size, changing in shape and becoming more deeply pigmented towards the thallus surface (Figs 5-8, 10). Inner cortical cells (cells of the first layer) are stellate, with an ovoid cell body 70-185 μm in diameter and radial arms (up to 40 μm in length) situated mainly in the plane of flattening (Fig. 8). Inner cortical cells are connected by secondary pit connections and form a network parallel to the surface of the frond, and are also



Figs 5-9. Vegetative structure of *Kallymenia lacerata.* mf, medullary filament; 1st, 2nd, 3rd, 4th, cortical layer arrangement. **5-6.** Cross sections of the blade (HGI-A 4776, 5300). **7.** Outer cortical cells in surface view forming a rosette around the less pigmented cells of the third cortical layer (HGI-A 4040). **8.** Cortical stellate cell of the 1st central layer (HGI-A 6362). **9.** Medullary stellate cell with arms situated distally (arrowheads) (HGI-A 4004). Scale bars = 75 μm (Fig. 5), 50 μm (Figs 6-9).

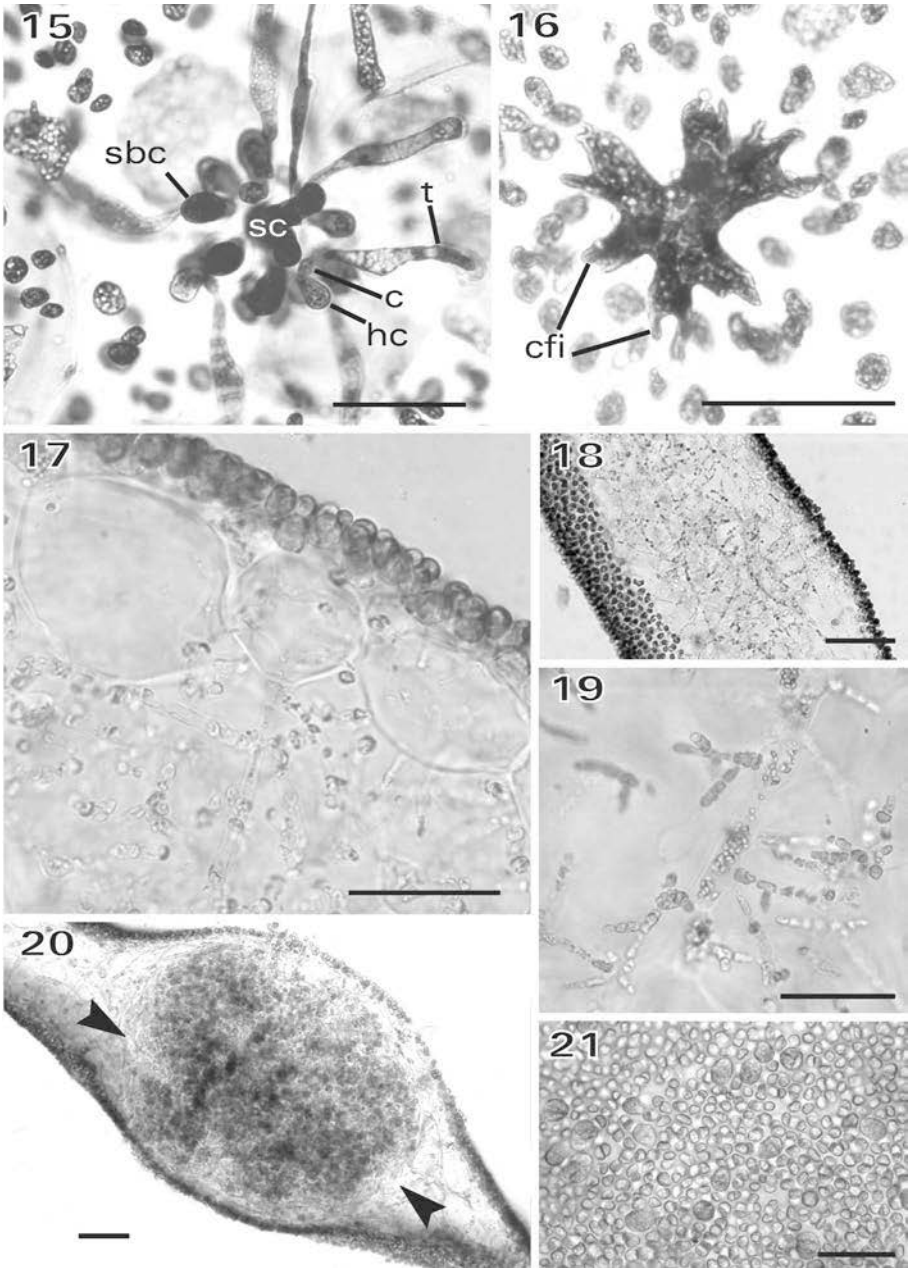
usually connected to the medullary filaments. Cells of the second layer of cortical cells are rounded or slightly stellate, hyaline, with a rounded or ovoid cell body (20-90 μm in diameter) connected with the other cells through slightly protruding points of junction, and thus forming a network parallel to the thallus surface. The third cortical layer is composed of rounded, pigmented cells (8-20 μm in diameter) lacking secondary pit-connections. Finally, outer cortical cells (4-12 μm diameter in surface view) are rounded, highly pigmented, spreading and forming rosettes around cells of the subsurface layer (Fig. 7). The medulla is very lax, composed of a network of stellate cells immersed in a gelatinous matrix and a few secondary filaments derived from the inner cortical cells (Figs 5-6, 9-11). Secondary medullary filaments, derived from the inner cortical cells, are simple or branched, composed of one or more cells, and usually hyaline, but if they contain floridean starch, they can be brownish (Fig. 6). They are very scarce in young parts of the thallus or in young thalli (Fig. 5), but become common at maturity (Fig. 6). Stellate medullary cells are hyaline, with an enlarged cell body (70-240 μm in length) and arms (up to 120 μm long) situated at distal parts of the cell (Fig. 9); these cells are connected and form a network parallel to the thallus surface, but they can be also connected to the medullary filaments or to the inner cortical cells.

Reproduction: Thalli are monoecious. Spermatangia are formed in sori to 400-1200 × 145-340 μm, scattered near the upper and median parts of the thallus. Spermatangial sori develop to one side of the cortex only, and are elongated, with an irregular margin. Spermatangial mother cells (25-30 μm long) are borne on cells of the outer cortex and cut off single, rounded spermatangia (2-6 μm in

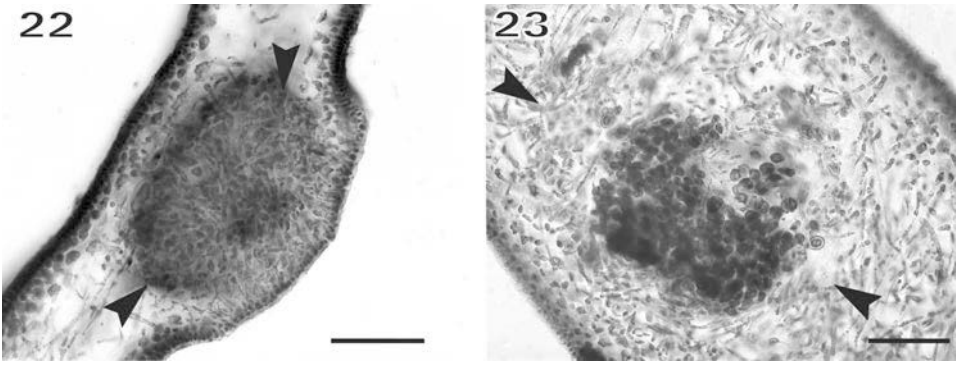


Figs 10-14. Drawings of the vegetative and reproductive structures of *Kallymenia lacerata.* c, carpogonium; cc, cortical cell; hc, hypogynous cell; sbc, subsidiary cell; sc, supporting cell; s, spermatangium; smc, spermatangium mother cell; t, trichogyne. **10.** Cross-section of the thallus (HGI-A 4776). **11.** Cross-section through a sorus of spermatangia (HGI-A 4784). **12.** Young carpogonial branch system with rounded or ovoid subsidiary cells and young trichogynes (HGI-A 5301). **13.** Mature carpogonial cell system with irregularly shaped subsidiary cells and well developed trichogynes (HGI-A 5301). **14.** Auxiliary cell system arising from an inner cortical cell and developing through the medulla (HGI-A 5301). Scale bars = 50 μm.

diameter) by a transverse or oblique division (Fig. 11). Plants are probably non-procarpic. Carpogonial branch systems arise on cells of the inner cortex and develop towards the medulla, and consist of a rounded supporting cell (up to 25 μm in diameter) that bears both several subsidiary cells that are rounded when young (Fig. 12) but irregular in shape at maturity (Figs 13, 15), and several three-celled carpogonial branches (Figs 12-13, 15); the carpogonium has a simple or occasionally bifurcated trichogyne (Fig. 13). Not all carpogonial branches mature at the same time. Auxiliary cell systems (up to 25 μm in diameter) are also situated on the inner cortical cells and develop through the medulla; they consist of a rounded or ovoid supporting cell that bears up to 8 rounded subsidiary cells (Fig. 14). After presumed fertilization, the supporting cell of the carpogonial



Figs 15-21. Light photomicrographs of a female gametophyte and a tetrasporophyte of *Kallymenia lacerata*. c, carpogonium; cfi, connecting filament initial; sc, supporting cell; sbc, subsidiary cell; t, trichogyne. **15.** Mature carpogonial cell system (HGI-A 5301). **16.** Aborted fusion cell (HGI-A 5301). **17-19.** Septate filaments filling the medulla (HGI-A 5301). **20.** Cross section of a mature gonimoblast surrounded by septate filaments (arrowheads) (HGI-A 5301). **21.** Tetrasporangia in surface view (H 2902). Scale bars = 50 μm (Figs 15-17, 19, 21), 100 μm (Figs 18, 20).



Figs 22-23. Light photomicrographs of cross-sections of gonimoblasts of *Kallymenia reniformis* surrounded by septate filaments (arrowheads) (HGI-A 2603; Montedor, Portugal; 27/9/99; coll. J. Cremades). Scale bars = 250 μm (Fig. 22), 100 μm (Fig. 23).

branch system seems to fuse with the subsidiary cells forming a stellate fusion cell, but these structures are very rare and the ones we have observed were mostly an aborted stage of a fusion cell, instead of a typical fusion cell (Fig. 16). In addition, we have never observed either a connecting filament connected to the auxiliary cell system or the initial development of the gonimoblast. In fertile parts of the thallus, some subsidiary cells from either carpogonial branch systems or auxiliary cell systems develop uniseriate, septate and branched filaments. These filaments extend and successively connect carpogonial cell systems, auxiliary cell systems and vegetative cells forming a large network that entirely fills the medulla of the plant (Figs 17-19). This network usually surrounds or is intermixed with gonimoblast filaments (Fig. 20), but sometimes neither gonimoblast filaments nor carpospores are present within it (Fig. 18). Gonimoblasts (440-1200 μm in diameter) grow through the medulla, swelling the thallus (Fig. 20); an ostiole is absent and carposporangia are released through the broken cortex; carposporangia (12-14 μm in diameter) occasionally germinate *in situ*. Tetrasporangia (15-20 μm in diameter) are scattered over the thallus in the outer cortex and are rounded and cruciately divided (Fig. 21).

DISCUSSION

The morphology and vegetative and reproductive structures of *Kallymenia lacerata* are similar to those of *K. reniformis*, the type species of the genus, differing mainly in: *i)* the shape and length of the blade (flat, sessile fronds arising from a small discoid holdfast, simple or lobed when young and laciniate when adult, up to 9 cm in length in *K. lacerata*, and fronds which are flat, sessile or shortly stipitate, undivided, reniform, up to 30 cm in length in *K. reniformis*), *ii)* the number of cortical layers (4 in *K. lacerata* and up to 6 in *K. reniformis*), *iii)* the arrangement of the outer cortical cells (forming rosettes in *K. lacerata* and arranged compactly in *K. reniformis*), *iv)* the medullary cells (with an enlarged cell body and arms situated distally in *K. lacerata* and ganglionic with radial arms in *K. reniformis*) and *v)* the fact that in *K. lacerata* no connecting filaments have yet been observed (Norris, 1957; Vergés, 2001; this work).

Table 1. Vegetative and reproductive characteristics of *Kallymenia lacerata* obtained from bibliographic references and from this study (* = from illustrations of the authors; — = missing data).

	Feldmann, 1942	*Huvé & Passelaigue, 1970*	*Codomier, 1971*	*This study*
Habit and vegetative structure				
Thallus thickness (μm)	180-200	185-400	200-350	170-280
Number of cortical layers	3-4*	—	4	4
First cortical layer				
Length of cell body (μm)	50-100	—	100-120	70-185
Second cortical layer				
Length of cell body (μm)	40-60	—	50-80	20-90
Third cortical layer				
Length of cell body (μm)	—	—	12-40	8-20
Fourth cortical layer				
Length of cell body (μm)	7-10	—	7-10	4-12
Medullary cells	—	—	Voluminous	Elongated
Length of cell body (μm)	—	—	150-160	70-240
Arm arrangement	—	—	—	Distal
Arm length (μm)	—	—	< 50	Up to 120
Reproductive characteristics				
Spermatangia	—	—	—	In sori
Diameter (μm)	—	—	—	2-6
Carpogonial branch system	—	—	—	Polycarpogonial
Diameter (μm)	—	—	—	80
Supporting cell diam. (μm)	—	—	—	Uo to 25
Auxiliary cell system diameter (μm)	—	—	—	Up to 25
Gonimoblast diameter (μm)	1000	—	—	440-1200
Carposporangia diameter (μm)	12-15	—	—	12-14
Tetrasporangium division	—	Cruciate	Cruciate	Cruciate
Tetrasporangium diameter (μm)	—	—	13-18	15-20

Our results on the morphology and vegetative structure of *K. lacerata* agree with other surveys of this species (Feldmann, 1942; Huvé & Passelaigue, 1970; Codomier, 1971, 1972; Table 1), although Huvé & Passelaigue (1970) and Codomier (1971, 1972) observed thalli that were larger in transverse section (< 400 μm and < 350 μm, respectively). The cells of the first and second layer of cortical cells measured by Feldmann (1942) and Codomier (1971, 1972) were considerably smaller (< 100 μm and < 120 μm, respectively) than those observed in this study (< 185 μm), and the same is true for cells of the second layer of cortical cells measured by Feldmann (1942) (< 60 μm) and those measured by us (< 90 μm); the diameter of cells of the third cortical layer was greater (< 40 μm) in Codomier (1971; 1972) than in our study (< 20 μm), and medullary cells had a smaller body (< 160 μm) and arms (< 50 mm) in Codomier (1971; 1972) than in our study (< 230 μm and < 120 μm, respectively). In our opinion, these are minor differences and must not be considered important, as they can be caused by the direction of sections as well as the age of the plant.

Table 2. Comparison of the Mediterranean species of *Kallymenia*.

Character	*K. reniformis*	*K. feldmannii*	*K. lacerata*	*K. patens*	*K. requienii*	*K. spathulata*
Thallus	Simple and reniform	Simple to lobed	Laciniate	Di-or trichotomously divided with bifurcated axes	Simple to lobed	Simple with proliferations
Maximum size (cm)	30 × 20	3.5 × 5.5	9 × 14	10 × 9.5	5 × 8	20 × 6
Stipitate	Yes or not	No	No	No	No	No
Cross-section (µm)	120-480	110-380	170-400	150-250	110-240	180-230
Cortical layers	4-5 (-6)	4-5	4	5	4-5	5
Outer cortical cell shape	Irregularly	Rounded / Ovoid	Rounded / Ovoid	Irregularly	Irregularly	Irregularly
Outer cortical cell arrangement	Compactly	Forming a rosette	Forming a rosette	Compactly	Compactly	Compactly
Maximum inner cortical cell length (µm)	< 60	< 100	< 185	< 70	< 60	< 30
Medullary cells	Stellate-ganglionic	Stellate	Elongate-stellate	Stellate-ganglionic	Stellate-ganglionic	Stellate-ganglionic
Colour	Yellow	Hyaline	Hyaline	Yellow	Yellow	Yellow
Body cell shape	Round	Round	Oblong	Round	Round	Round
Arms arrangement	Radial	Radial	Distal	Radial	Radial	Radial
Spermatangia	In sori	In sori	In sori	Unknown	Unknown	Unknown
Carpogonial cell system	Polycar-pogonial	Polycar-pogonial	Polycar-pogonial	Unknown	Monocar-pogonial	Unknown
Fusion cell	Present	Present	Present	Unknown	Present	Unknown
Auxiliary cell system	Present	Present	Present	Unknown	Present	Unknown
Gonimoblast initial	On connecting filaments / vegetative cells	On connecting filaments	Unknown filaments	Unknown	On connecting	Unknown
Tetraspo-rangia	Cruciate, zonate or irregular	Cruciate	Cruciate	Probably cruciate	Cruciate	Cruciate
Distribution	N Atlantic, NE Pacific, Indian, Mediterranean	W Mediterranean	Mediterranean	W Mediterranean	Mediterranean	Mediterranean
References	Norris, 1957; Hommersand & Ott, 1970; Codomier, 1971, 1972; Vergés, 2001	Codomier, 1971; 1972; Vergés, 2001	Huvé & Passelaigue, 1970; Codomier, 1971, 1972; Vergés, 2001; this study	Codomier, 1971, 1972; Vergés, 2001	Codomier, 1971, 1972; Vergés, 2001	Codomier, 1971, 1972; Vergés, 2001

The combination of the vegetative characters pointed out by Codomier (1968, 1971, 1972) (morphology, shape of the outer cortical cells and length of the larger cells of the inner cortex), added together with the number of cortical cell layers, the medullary cell shape and the female reproductive structures (this work), clearly differentiates this species from the rest of the species of *Kallymenia* found in the same geographical area (Table 2). *K. lacerata* is the only species with a laciniate thallus, as blades are simple and reniform in *K. reniformis*, simple to lobed in *K. requienii* and *K. feldmannii*, simple with proliferations in *K. spathulata,* and di- or trichotomously divided in *K. patens*. Outer cortical cells are rounded or ovoid and are spread and arranged in rosettes around the subcortical layer in *K. lacerata* and in *K. feldmannii,* whereas the other species have these cells arranged compactly (when sterile) and irregularly shaped. Inner cortical cells are stellate in all the species, but the maximum body cell length is found in *K. lacerata* (to 185 μm). *K. lacerata* is the only species that always has 4 cortical layers of cells (*K. reniformis* has 4 to 6, *K. feldmannii* and *K. requienii* have 4 or 5, and *K. patens* and *K. spathulata* always have 5). *K. lacerata* is also the only species with elongated stellate cells with distally arranged arms, since *K. reniformis*, *K. patens*, *K. requienii* and *K. spathulata* have stellate-ganglionic medullary cells, with a rounded cell body and radially arranged arms. Finally, while *K. lacerata, K. reniformis* and *K. feldmannii* are polycarpogonial, *K. requienii* is monocarpogonial, and the female reproductive systems of *K. patens* and *K. spathulata* are unknown (Table 2).

Kallymenia lacerata is similar to the three described species of the genus *Thamnophyllis* Norris: *T. pocockiae* Norris, *T. discigera* (J. Agardh) Norris and *T lacerata* Womersley *et* Norris (Norris, 1964; Womersley & Norris, 1971; Womersley, 1994). Indeed, morphologically, *K. lacerata* shares with these species a lacerate thallus and the enlarged, rounded cells that Norris (1964), Womersley & Norris (1971) and Womersley (1994) treat as medullary cells and Codomier (1972) and us (this work) regard as inner cortical cells. Nevertheless, in spite of the coincidence in these characters, *Thamnophyllis* has a very compact medulla whereas *K. lacerata* has a lax medulla, like that in other species of *Kallymenia* (Vergés, 2001). In addition *T. pocockiae* and *T. lacerata* possess a series of refractive medullary cells, with long arms radiating along the plane of the thallus surface and filled with a thick yellowish substance, which is absent in *K. lacerata*, a species having hyaline medullary stellate cells with short arms (up to 120 μm) arranged distally.

As in *K. lacerata,* several other species of *Kallymenia* have male reproductive structures located in sori (Table 2), including *K. reniformis* (Vergés, 2001), *K. feldmannii* (Vergés, 2001), *K. reniformis* f. *cuneata* J. Agardh (Tazawa, 1975), *K. sessilis* Okamura (Abbott & McDermid, 2002) and *K. westii* Ganesan (Schneider & Searles, 1991). Nevertheless, this character appears to be variable within the genus, since some species bear spermatangia scattered over the thallus surface [e.g. *K. pacifica* Kylin from the Pacific North America (Abbott, 1968) and *K. cribrosa* Harvey and *K. cribrogloea* Womersley *et* Norris (Womersley, 1994) from Australia.

Carpogonial branch systems of *K. lacerata* are very similar in morphology to those of *K. reniformis* and *Thamnophyllis pocockiae*; however, *K. reniformis* is fully polycarpogonial, whereas in *T. pocockiae* and *K. lacerata* some of the subsidiary cells lack carpogonial branches, a feature interpreted by Norris (1957) as representing a tendency toward the monocarpogonial condition. Moreover, *K. lacerata* doesn't develop all the carpogonial branches simultaneously and, consequently, when it is immature it can resemble a monocarpogonial species. According to Norris (1957, 1964), Womersley & Norris (1971) and Womersley (1994), the carpogonial branch systems in the genus *Kallymenia* are composed of

a supporting cell and one to several three-celled carpogonial branches surrounded by subsidiary cells. Codomier (1968, 1971, 1972) gave another interpretation of this structure in his studies of the Mediterranean *Kallymenia* species, pointing out that the carpogonial cell system was a "gonophore" composed of a supporting cell surrounded by subsidiary cells with some of these subsidiary cells supporting a two-celled carpogonial branch. In this study we interpret the female reproductive structure in accordance with R.E. Norris and H.B.S. Womersley.

The presence in *K. lacerata* of auxiliary cell systems similar to those described by Norris (1957) for *K. reniformis* (Table 2), and by Vergés (2001) in *K. feldmannii* and *K. requienii*, indicates that *K. lacerata* could be non-procarpic, but, as neither non-aborted fusion cells nor connecting filaments have been observed, this point remains unclear.

Secondary vegetative filaments surrounding the gonimoblast are also present around gonimoblasts of the type species of *Kallymenia*, *K. reniformis* (Figs 22-23), are present in *K. feldmannii* and *K. requienii,* and probably are the filaments illustrated by Norris (1964, fig. 26) in *Thamnophyllis pocockiae.*

With regard to the conspicuous network of septate filaments not associated with gonimoblasts observed here in *K. lacerata* (Figs 17-19), there was no evidence that carposporangia were previously formed and released in that area and, as such, these filaments cannot be remnant gonimoblast filaments.

The origin of the gonimoblasts in *K. lacerata* remains unknown. In *K. reniformis,* gonimoblast initials have been observed on the connecting filaments (Norris, 1957; Vergés, 2001), and also on vegetative cells (Hommersand & Ott, 1970), and in *K. feldmannii* and *K. requienii* gonimoblast initials have been sighted on the connecting filament (Vergés, 2001). According to our observations on these species, gonimoblast cells develop on the connecting filament but vegetative cells are connected to the connecting filament and also participate in the formation of the gonimoblast. In *K. lacerata*, the origin of the gonimoblast could be the same as in these species of *Kallymenia* or alternatively, it may be apomictic.

Fusion cells, connecting filaments and gonimoblasts are very scarce in fertile gametophytes of *K. lacerata*, and this makes us believe that fertilization may be very occasional.

Tetrasporangia are cruciate in all the Mediterranean *Kallymenia* species but *K. reniformis* has also zonate and irregularly divided tetrasporangia (Vergés, 2001).

In conclusion, the vegetative and reproductive characters of *K. lacerata* are typical for the genus and correspond to those of the type species. Vegetative structure is very useful for distinguishing species in *Kallymenia* (Codomier, 1971; Abbott & McDermid, 2002), in addition to reproductive characters. *K. lacerata* is distinguishable from the rest of the *Kallymenia* species in the Mediterranean by: a laciniate blade when adult, four layers of cortical present cells at all times, outer cortical cells arranged in rosettes, hyaline medullary cells with an enlarged cell body and arms situated distally, and a polycarpogonial branch system composed of a mixture of carpogonial branches and subsidiary cells.

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