

Biology and taxonomic identity of *ErythroGLOSSUM lusitanicum* (Delesseriaceae, Rhodophyta) from the Iberian Peninsula

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Abstract

ErythroGLOSSUM lusitanicum was originally described from sterile and tetrasporophytic material. The apical organization and the sexual structures have considerable relevance for classification of Delesseriaceae, and these are described here for the first time in this species. The range of morphological variability in some species of the genus *ErythroGLOSSUM* in Atlantic Europe has been broadened, requiring a revision of the taxonomic identity of *E. lusitanicum*. Reproductive characters observed in *E. lusitanicum* include: 1) procarps scattered over the blade surface and composed of a supporting cell bearing two 4-celled carpogonial branches and a single group of sterile cells; 2) carposporangia formed in chains; and 3) spermatangial sori consisting of two layers of spermatangial mother cells bearing spermatangia. These features, together with the *Phycodrys*-type apical organization, are in accordance with those described for the genus *ErythroGLOSSUM*. The main taxonomic features of *E. lusitanicum* that distinguish it from congeners in Atlantic Europe are thallus growth that occurs in each blade by means of a single apical cell located in the tip, and its turf forming habit.

Keywords: *ErythroGLOSSUM laciniatum*; *ErythroGLOSSUM lusitanicum*; *ErythroGLOSSUM sandrianum*; morphology; taxonomy.

Introduction

ErythroGLOSSUM lusitanicum Ardré (1970) was described from sterile and tetrasporophytic specimens collected at two localities in the north of Portugal, Montedor and Buarcos (Ardré 1970). The species was not reported again until the 1990s (Birje et al. 1995), but in the last

10 years new information has expanded its distribution along the Iberian Peninsula and the coast of Morocco. *ErythroGLOSSUM lusitanicum* has been observed in north-western Spain (Bárbara et al. 2003, 2005, 2006), Portugal (Araújo et al. 2003, Bárbara et al. 2006) and Morocco (Birje et al. 1995, Benhissoune et al. 2003). To date, only non-sexual plants have been reported and the tetrasporophytic stage has been described, based on the original description provided by Ardré (1970).

The genus *ErythroGLOSSUM* J. Agardh (1898), with the lectotype species *ErythroGLOSSUM schousboei* (J. Agardh) J. Agardh [=? *E. sandrianum* (Kützing) Kylin], is characterized by a combination of characters related to apical organization, presence of midribs, veins or nerves, position of tetrasporangial sori, and features of female structures (Maggs and Hommersand 1993, Wynne 1996, 2001, Yoshida and Mikami 1997). The apical organization and the sexual structures have great importance in the classification of Delesseriaceae, but they remain unknown in *E. lusitanicum*.

The genus *ErythroGLOSSUM* contains more than 10 species. The European Atlantic species are *E. lusitanicum* and *E. laciniatum* (Lightfoot) Maggs et Hommersand. A third species, *E. sandrianum* (Kützing) Kylin, originally described from material collected in Dalmatia, has been widely reported in the Mediterranean Sea (Athanasiadis 1985) and also along the European Atlantic coast (Feldmann 1954, Ardré 1970, South and Tittley 1986, Granja et al. 1992). However, its presence in the Atlantic region has been questioned by Maggs and Hommersand (1993) who also suggested that the holotype of *E. sandrianum* may be conspecific with *E. laciniatum*. Furthermore, Athanasiadis (1985) proposed synonymy between *E. sandrianum* and *E. schousboei* from Tangier, while a fifth poorly known species from the same area is *E. subcostatum* (J. Agardh) Ardré.

The broad concept of *ErythroGLOSSUM laciniatum* by Maggs and Hommersand (1993) included a wide range of morphological variation: under sheltered conditions, very broad, lobed blades reach 15–20 cm in width and margins are entire; there is little change in form throughout the season. On exposed coasts, young plants collected in May to early June are up to 2 cm in width and consist of entire or broadly lobed blades, sometimes with small marginal teeth. By July–August, all thalli have developed fringed apices and narrow marginal outgrowths; they are rarely more than 5–10 cm in total width (Maggs and Hommersand 1993: 223). Ardré (1970) reported both *E. lusitanicum* and *E. sandrianum* in Portugal and she proposed differentiating the species by the presence of stoloniferous branches and the thicker blades in *E. lusitanicum* [Ardré 1970: 184; “C’est à cette

espèce que j'aurais rattaché ces thalles (*E. sandrianum*), si ceux-ci n'étaient nettement plus épais que l'*E. sandrianum*: à 2–3 mm de l'apex, 50 μ d'épaisseur à la marge du thalle; 60–75 μ d'épaisseur à un niveau un peu inférieur. Les algues du Portugal que j'ai rapportées à l'*E. sandrianum*, ainsi que des échantillons conservés sous ce nom dans les Herbiers du Muséum qui proviennent de Dalmatie (ex herb. Roussel), de Minorque (9/1889 et 1891, leg. Rodriguez), sont plus minces puisque, même vers la base des thalles, l'épaisseur des ailes ne dépasse pas 40 μ ”].

The aim of this work is to provide an improved description of the vegetative features of *ErythroglOSSum lusitanicum* and to describe for the first time its sexual structures. A taxonomic revision of the generic status of this species and its taxonomic status among species of the genus from Atlantic Europe are also discussed on the basis of both vegetative and reproductive features. Finally, the habitat, reproduction, and distribution of *E. lusitanicum* along the Atlantic Iberian coast are also described.

Materials and methods

Sampling and preparation of material

Material was collected in the intertidal and subtidal zones between 2002 and 2007 at 74 sites along the Atlantic coasts of the Iberian Peninsula, from northwestern Spain to southern Portugal. The material was preserved in either 4% formalin seawater or KEW solution (40%), ethanol (70%), 40% seawater, 10% glycerine and 10% formaldehyde (4%) at 4°C and stored in the dark until analysis.

Specimens were stained in a mixture of 1% aniline blue, 1% acetic acid, 50% Karo® Syrup (ACH Foods, Memphis, TN, USA) and 48% distilled water (Millar and Wynne 1992). Preserved specimens were deposited in the herbarium of the Universidad de Santiago de Compostela (SANT) and the herbarium of Algarve (ALGU). Our study included herbarium material of *ErythroglOSSum lusitanicum* from SANT and type material collected by Ardré and stored at the PC herbarium. The single specimen designated by Ardré (1970, pl. 55, fig. 1) as holotype (from Buarcos leg. Moraes) was not found in the Coimbra Herbarium (COI). Herbarium abbreviations follow Holmgren et al. (1990).

Selected specimens

Spain (1) Playa de Estaño, lower littoral, on rocks covered by sand, 18/04/2007, SANT-Algae 19841. (2) Playa de Aguilar, lower littoral, on rocks covered by sand, 17/04/2007, SANT-Algae 19830. (3) Playa del Sarello, lower littoral, on rocks covered by sand, 02/02/2006, SANT-Algae 16843 (tetrasporangia), 16844. (4) Playa de las Catedrales, lower littoral, on rocks covered by sand, 20/09/2005, SANT-Algae 16539. (5) Peinzás, lower littoral, on rocks covered by sand, 26/12/2007, SANT-Algae 19786. (6) Playa de San Román, lower littoral, on rocks

covered by sand, 31/01/2006, SANT-Algae 16869; subtidal (-1 m), on rocks covered by sand, 20/02/2008, SANT-Algae 19791 (tetrasporangia). (7) Playa de Pantín, pool in the lower littoral, on rocks covered by sand, 26/10/2007, SANT-Algae 19531 (spermatangia). (8) Cala de Canabal, subtidal (-3 m), on rocks covered by sand, 08/10/2005, SANT-Algae 16490 (tetrasporangia). (9) Ártabra, lower littoral, on rocks covered by sand, 09/02/2005, SANT-Algae 17897; 09/03/2005, SANT-Algae 17285 (tetrasporangia). (10) Playa de Leira, pool in the lower littoral, on rocks covered by sand, 27/01/2001, SANT-Algae 12932. (11) Cambre, subtidal (-1 m), on rocks covered by sand, 18/02/2008, SANT-Algae 19787. (12) Playa de Barizo, lower littoral, on rocks covered by sand, 29/09/2004, SANT-Algae 15252. (13) Ensenada de Barda, subtidal (-1 m), on rocks covered by sand, 24/01/2003, SANT-Algae 13899 (tetrasporangia). (14) Camelle, lower littoral, 20/03/2007, SANT-Algae 19007. (15) Playa de Lourido, lower littoral, on rocks covered by sand, 01/02/2006, SANT-Algae 17008 (tetrasporangia); subtidal (-1 m), on rocks covered by sand, 13/02/2008, SANT-Algae 19789 (tetrasporangia). (16) Ensenada Bornalle, subtidal (-14 m), on maërl beds and gravel, 01/06/2006, SANT-Algae 18226. (17) Isla de Noro, subtidal (-4 m), on maërl bed and gravel, 22/06/2005, SANT-Algae 18557. (18) Isla de Ons, subtidal (-14 m), on maërl bed, 05/06/2006, SANT-Algae 18057. (19) Con de Pego, subtidal (-4 m), on maërl bed, 25/08/2005, SANT-Algae 16790.

Portugal (20) Áncora, subtidal (-5 m), 17/09/2003, SANT-Algae 15583 (tetrasporangia and cystocarps); 14/9/2003, ALGU 1290, 1291, 1292 (tetrasporangia). (21) Montedor, pool on lower littoral covered by sand, 07/02/1997, SANT-Algae 9033 (tetrasporangia and cystocarps). (22) Viana do Castelo, rocks on lower-middle littoral, 28/09/1999, SANT-Algae 10474; 15/9/2003, ALGU 10176. (23) Cepães, lower littoral, on rocks covered by sand, 14/11/2004, SANT-Algae 15584 (tetrasporangia and spermatangia). (24) Esposende lower littoral, on rocks covered by sand, 09/02/1997, SANT-Algae 9065. (25) Leça de Palmeira, lower littoral, on rocks covered by sand, 16/11/2004, SANT-Algae 16352 (tetrasporangia). (26) Miramar, lower littoral, on rocks covered by sand, 11/01/2005, SANT-Algae 19406 (tetrasporangia). (27) Figueira da Foz, intertidal, and subtidal, 19/9/2003, 20/9/2003, ALGU 6614, 6615, 6616. (28) São Martinho do Porto, intertidal, and subtidal, 14/8/2003, ALGU 2548, 2551. (29) Baleal, subtidal, 9/08/2003, ALGU 9529. (30) Peniche, intertidal, and subtidal, 11/08/2003, 12/08/2003, ALGU 3815, 3816, 3817. (31) Queimado, pool on lower littoral covered by sand, 25/05/2005, SANT-Algae 15732 (tetrasporangia and cystocarps). (32) Sagres-Ingrina, intertidal, and subtidal, 14/02/2003, 21/08/2004, ALGU 10884, 10885. (33) Lagos, intertidal, and subtidal, 26/06/2003, 27/06/2003, ALGU 8493, 8494, 8495, 8496 (tetrasporangia). (34) Carvoeiro, intertidal, and subtidal, 13/05/2003, 14/05/2003, 15/05/2003, ALGU 5254, 5255, 5256, 5268 (tetrasporangia). (35) Armação de Pera, subtidal (-15 m), on rocks and maërl beds, 06/06/2007, SANT-Algae 19402. (36) Olhos d'Água, pool on lower littoral covered by sand, 06/05/2005, SANT-Algae 15731.

Results

Vegetative morphology

Thalli 3–5(7) cm long, consisting of a basal discoid holdfast bearing a stipe, from which arise irregular lateral elongate proliferations and erect ovate to oblanceolate blades with a midrib (Figure 1). Some proliferations have discrete patches of rhizoids, and thalli form elaborate creeping rhizomatous bases. As a mode of regeneration, old blades bear young blades irregularly located along margins of basal parts and on broken tips. Blades are brownish-pink.

Stipe cylindrical to compressed, 2–17 mm long and 0.3–1.3 mm diameter. The thallus is usually alternately branched and produces blades or proliferations from which rhizoids arise occasionally from the margin. Rhizoids are 70–1400 μm long and 70–200 μm in diameter.

Blades arise from a short stipe that is cylindrical to compressed and up to 6 mm long and 1 mm in diameter. Each blade grows by means of a single apical cell (occasionally there are 2 apical cells, see Ardré 1970, pl. 19, fig. 1), which divide transversely cutting off cells proximally. Cells of the primary cell row undergo intercalary divisions and also produce second-order cell rows laterally. Third-order cell rows are cut off abaxially from the second-order rows (Figure 2A, B).

The morphology and sizes of blades are variable. Young blades are small and simple, and from ovate to oblanceolate (Figure 2C, D). Older blades are oblanceolate, to 27 mm long and 6 mm wide, usually simple but sometimes dichotomously branched at the apical part. Tips of old blades are usually broken and bear one to several new blades with short stipes (Figure 2E, F). Margins are entire or with short proliferations, sometimes pro-

ducing new blades or rhizomatous proliferations. There are (1) 2–4 (6) orders of successive blades.

Blades are monostromatic except in the midrib region. Monostromatic areas are (30) 40–65 (100) μm thick in median parts. The midrib is 3-celled and (35) 45–100 (140) μm thick in the apical parts (Figure 2G) and up to 7 cells and (50) 80–180 (250) μm thick in basal parts (Figure 2H–J). The cortication in the middle part of the blade starts approximately 600–1000 μm below the apex and is evident near the basal part, where it is 1.2 mm wide. Microscopic veins or nerves are absent.

In surface view, cells are polygonal (15) 20–70 (100) \times (15) 20–50 (60) μm . Plastids are discoid to bacilloid.

Reproductive morphology

Tetrasporangial sori are located along both sides of the midrib in basal and median portions of blades, or occasionally in an apical position (Figure 3A–E), sometimes confluent over the midrib in young blades. Sori are initially oval, usually several sori per blade (Figure 3B, C), becoming confluent later and acquiring an elongate outline (Figure 3D). Sorus thickness (50)–100–150–(190) μm , with two rows of tetrasporangia (each on one side of the blade) (Figure 3G). Tetrahedral sporangia ellipsoid, 22–53 \times 30–63 μm (Figure 3F).

Gametophytes are dioecious. Male sori are located on both sides of the midrib in basal and median parts of blades, covering the entire surface of apical parts of blades or the entire surface of young blades (Figure 4A–C). Sorus oval to elongate, 600–3000 μm long and 55–600 μm wide, consisting of two layers of rounded to quadrangular spermatangial mother cells, 6–7 μm long

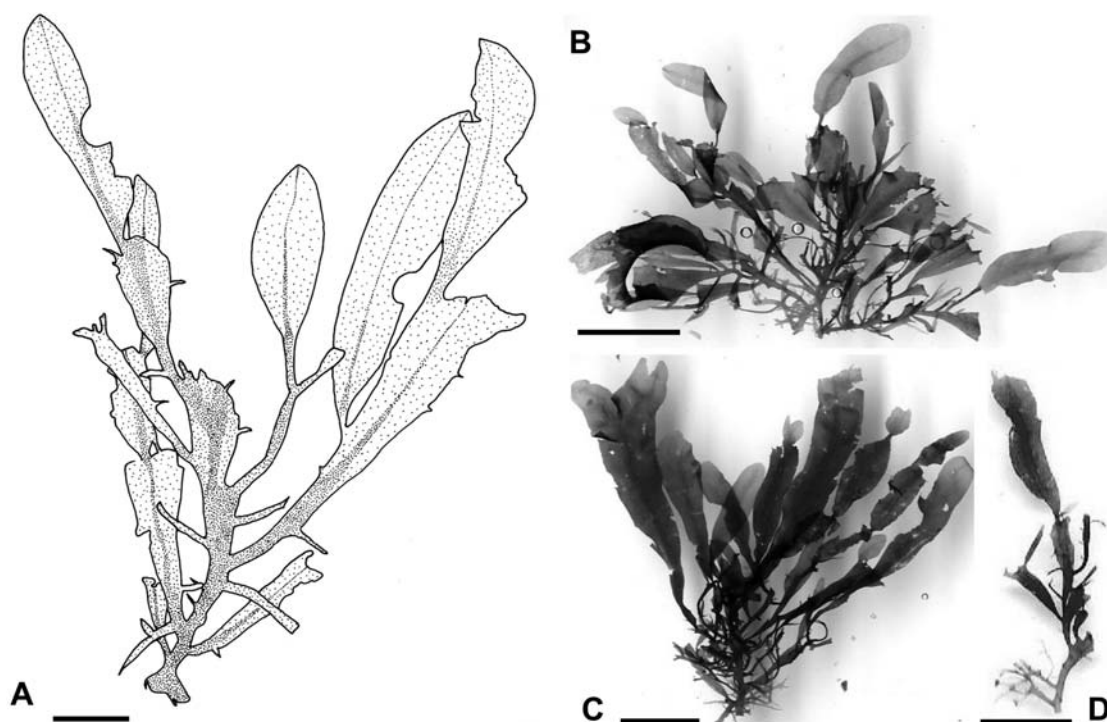


Figure 1 *Erythroglossum lusitanicum*: habit of vegetative thallus (A–D). Scale bars: A, D=2 mm, B, C=1 cm.

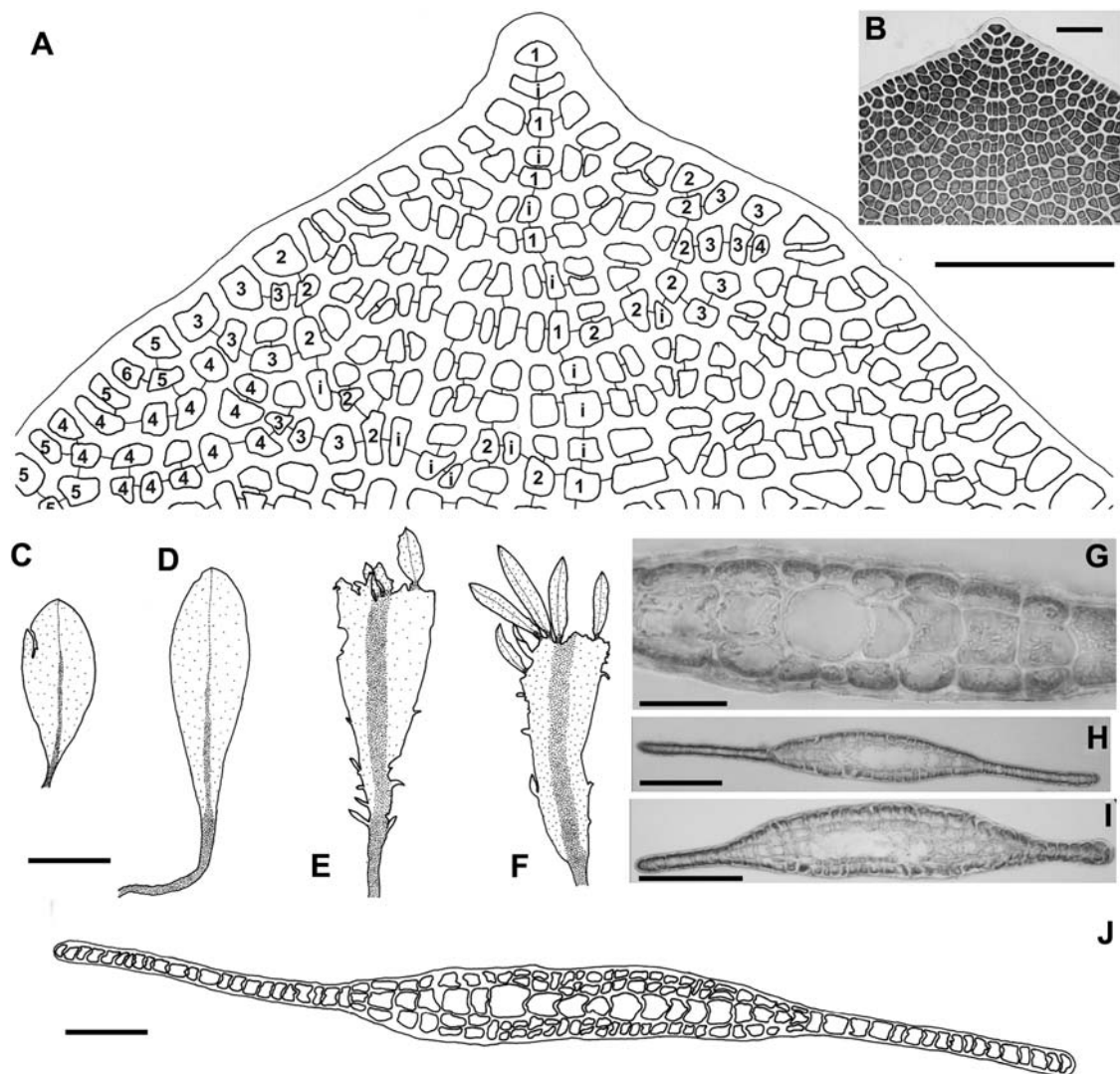


Figure 2 *Erythroglossum lusitanicum*: vegetative plants.

(A, B) Apical organization. 1–5: first to fifth-order cells, respectively; i: cell resulting from intercalary division. (C, D) Young blades. (E, F) Old blades with marginal proliferations and new blades arising from the broken parts of the apex. (G–J) Cross-section of a blade showing the midrib in the apical part (G), the midrib and the monostromatic wing in the apical part (H) and the midrib and the monostromatic wing in the median and basal part (I–J). Scale bars: A, B, G=50 μm , C–F=5 mm, H, I=300 μm , J=150 μm .

and 5–6 μm wide (each on one side of the blade), bearing 2 (3) elongate spermatangia, 5–9 μm long and 2.5–3.5 μm wide (Figure 4D–G).

Procarys are scattered over the monostromatic areas of blades, consisting of a supporting cell, a group of 2–4 sterile cells and two opposite carpogonial branches, each consisting of 4 cells (Figure 5C). Cystocarps are scattered over blades (Figure 5D, E), 275–430 μm in diameter, with a 40–60 μm diameter ostiole. Gonimoblast filaments are branched, and from these arise ovoid carposporangia 23–30 μm in diameter arrayed in short chains (Figure 5F, G).

Habitat and reproduction

Erythroglossum lusitanicum occurs mainly on wave-exposed coasts at lower intertidal to upper subtidal (down to 2 m depth) levels, where it forms dense turfs on sand-covered rocks and pools (Figure 6A). These turfs usually have basal parts buried by sand, and only the

apices of the largest blades are emergent. The turfs usually contain other species typical of this habitat, such as *Pterosiphonia ardreana* Maggs et Hommersand, *P. pennata* (C. Agardh) Sauvageau, *Jania longifurca* Zanardini, *Rhodothamniella floridula* (Dillwyn) J. Feldmann, *Hypoglossum hypoglossoides* (Stackhouse) Collins et Hervey and *Ptilothamnion sphaericum* (P. Crouan et H. Crouan ex J. Agardh) Maggs et Hommersand. *Erythroglossum lusitanicum* also grows scattered on maërl beds up to 20 m depth, where it is a frequent species but with lower abundance and never forming turfs.

Erythroglossum lusitanicum can be found throughout the year. Tetrasporangial thalli are frequent on sand-covered rocks; they were present in 42% of samples collected. The sexual structures are rare. Male gametophytes were collected only twice (October and November), whereas female gametophytes were collected in 5 samples in February, May, and September. Reproductive structures were never present in the samples from maërl beds.

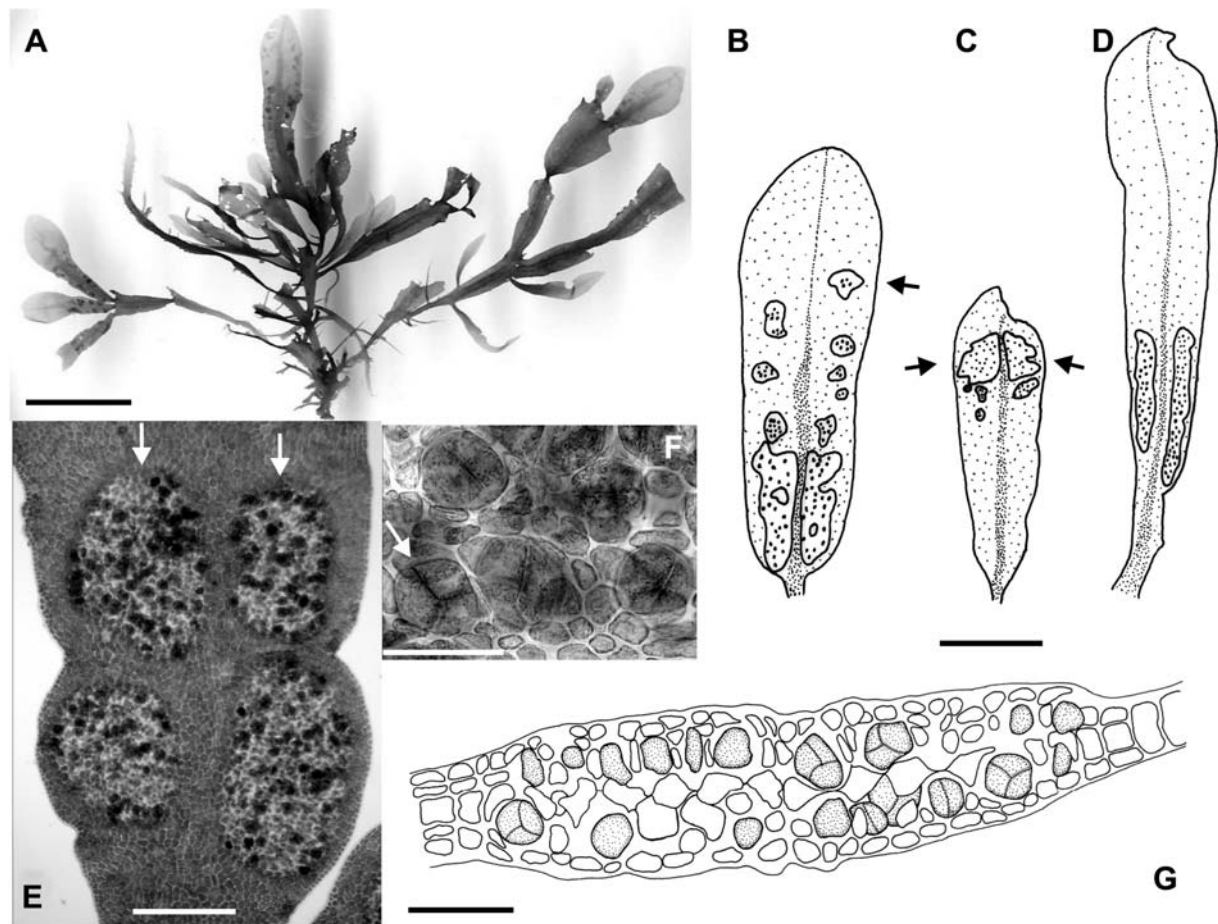


Figure 3 *ErythroGLOSSUM lusitanicum*: tetrasporangial plants.

(A) Habit of tetrasporangial thallus. (B–D) Tetrasporangial sori (arrows) located on both sides of midrib. (E) Tetrasporangial sori (arrows) in superficial view. (F) Tetrahedral sporangia (arrow) in superficial view. (G) Cross-section of tetrasporangial sori. Scale bars: A=1 cm, B–D=3 mm, E=500 μm , F, G=100 μm .

Distribution

ErythroGLOSSUM lusitanicum has been reported from 21 sites on the Atlantic coast of the Iberian Peninsula and, recently, it has also been found in 53 new sites (Figure 6B). It has been reported in Morocco (Birje et al. 1995, Benhissoune et al. 2003). Unfortunately, the material from Morocco could not be studied for this work, because it is not available in a public herbarium (Benhissoune et al. 2003).

Discussion

The Iberian material shows the features of the genus *ErythroGLOSSUM* described by Maggs and Hommersand (1993), Yoshida and Mikami (1997), and Wynne (1996, 2001): a) growth by means of transverse divisions of the apical cell of each axis; b) intercalary cell divisions occurring in the cells of the first- and higher-order cell rows; c) apical organization of the *Phycodryis*-type and involving second-order cell rows producing third-order cell rows abaxially; d) blades with midribs, veins, or nerves; e) tetrasporangial sori arranged along blade margins; f) procarps of the *Polyneura*-type, consisting of a supporting cell, two carpopogonial branches and a group of sterile

cells; g) carposporangia formed in short chains. The observation of *Phycodryis*-type apical growth and procarps of *Polyneura*-type in *E. lusitanicum* precludes the possibility that this species belongs to the genus *Valerimaya* A.J.K. Millar et M.J. Wynne (Millar and Wynne 1992), which contains three species whose thallus outlines are very similar to *E. lusitanicum*.

The sexual structures (described for the first time in this paper) are in agreement with the genus *ErythroGLOSSUM* (Kylin 1924, 1956, Mikami 1976, 1977, Maggs and Hommersand 1993, Yoshida and Mikami 1997). The procarps of *E. lusitanicum* are scattered over monostromatic areas of the blades and are of the *Polyneura*-type. The carposporangia are formed in short chains. The spermatangial sori are composed of two layers of mother cells (each on one side of the blade) bearing spermatangia and are located along the thallus margins. The spermatangial sori in *E. lusitanicum* cover the entire surface of young blades or the apical parts of the blades where the midrib is not well developed.

The Iberian material of *ErythroGLOSSUM lusitanicum* collected from the intertidal to the lower sublittoral zone on sand-covered rocks had relatively little morphological variation. The specimen selected as type by Ardré is an individual that is particularly well developed and prolific (Ardré 1970, pl. 55, fig. 1); it was collected by

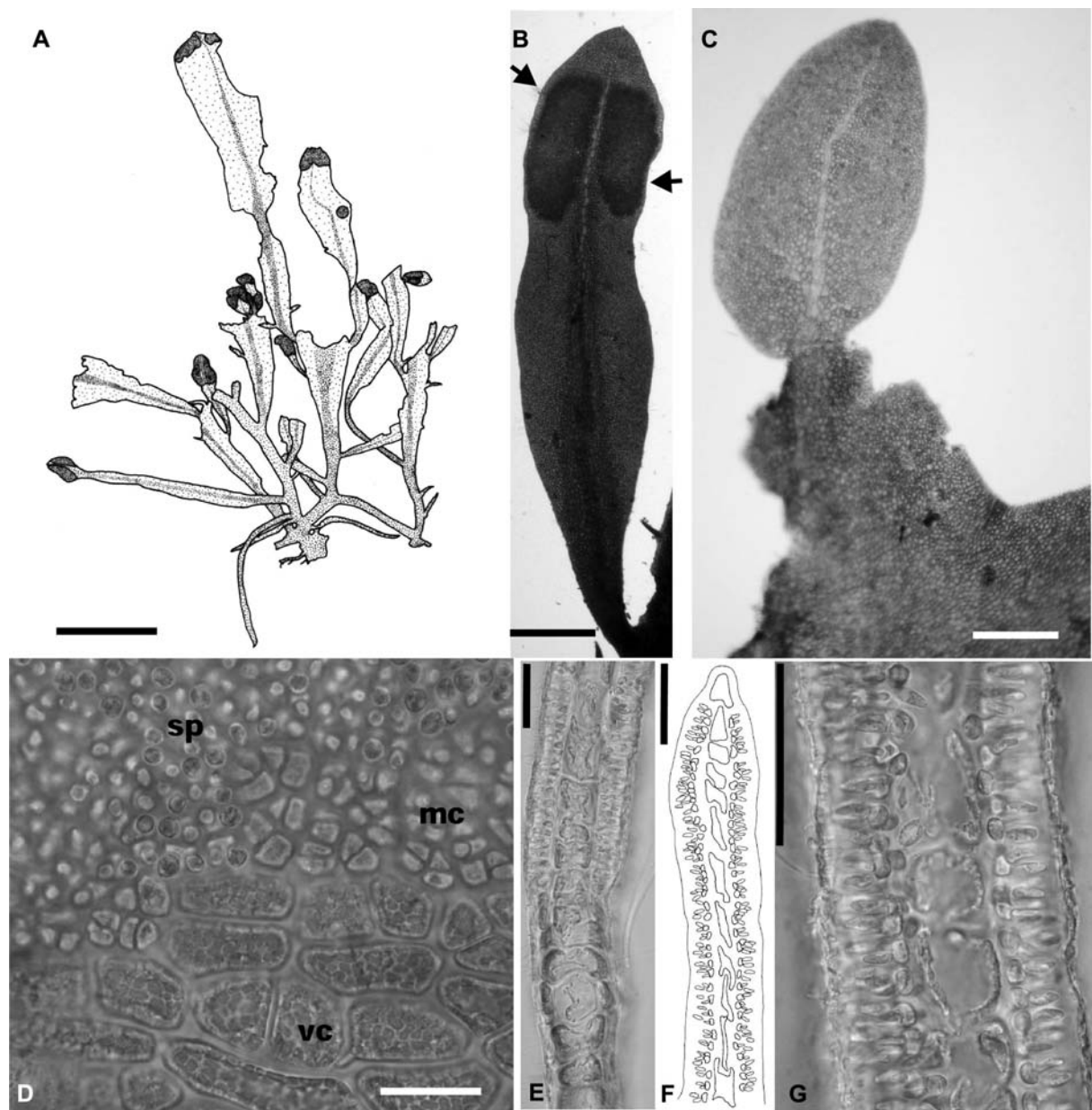


Figure 4 *Erythroglossum lusitanicum*: male plants.

(A) Habit of spermatangial thallus. (B) Blade with spermatangial sori (arrows) located at the apex and on both sides of the midrib. (C) Spermatangial sori covering whole surface of a young blade. (D) Spermatangial sori in surface view showing vegetative cells (vc), mother cells (mc), and spermatangia (sp). (E–G) Cross-section of tetrasporangial sori. Scale bars: A=5 mm, B=2 mm, C=800 μm , D=20 μm , E–G=50 μm .

Moraes in 1929 and originally labeled as *Rhodymenia palmata* (Linnaeus) Greville. This specimen was said to be deposited at the herbarium of Coimbra (COI), but it was not found during exhaustive revision of COI. The other type material, collected by Ardré in Montedor, is stored at the Herbarium of Paris (PC). This collection consists of 5 sheets and 12 slides (PC0122679–122689). In the absence of the holotype, we propose as lectotype the sheet PC0122679, which contains several plants of *E. lusitanicum* (Figure 6C), some of them with tetrasporangia [Lectotype: PC 0122679, Montedor (Portugal), 25/3/1963, leg. Ardré]. The thalli of Montedor's collection are smaller and have fewer proliferations than the specimen from Buarcos.

The thalli collected from maërl beds are usually smaller and with a less developed prostrate system (often the thalli are composed of a single blade attached to maërl and they sometimes have an extremely proliferous habit) than those from sandy bedrock. These morphological differences seem to be related to the habitat, as maërl beds are mobile substrata wherein the dominant epiflora is composed of crustose and creeping species that form tangles of maërl (V. Peña, personal communication), whereas on sand-covered rocks, turfs with an extensive prostrate system are the predominant morphology (Stewart 1983, Kendrick 1991, Airoldi 2001, Balata et al. 2005). In spite of its peculiarities, the material from maërl beds has the main features of the species.

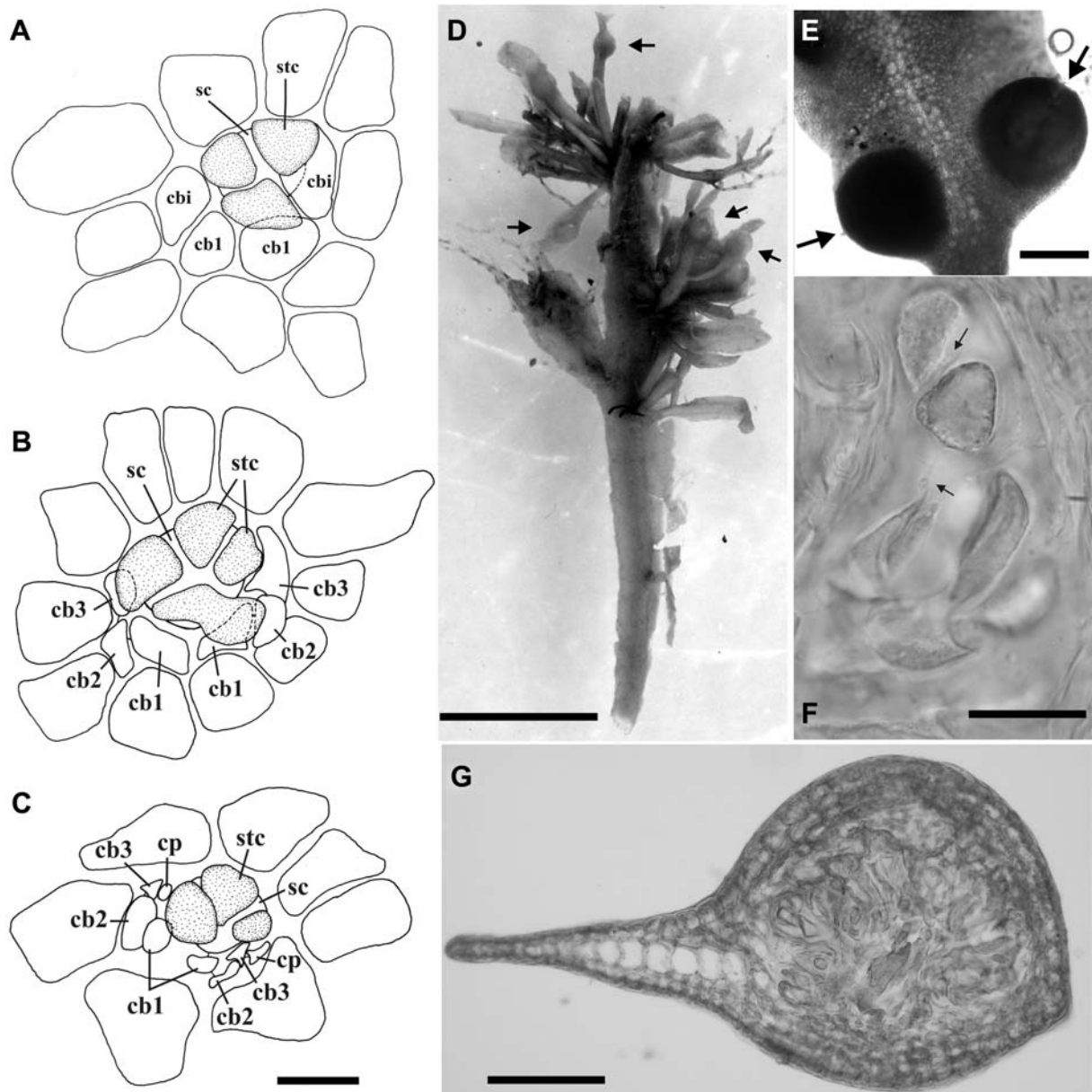


Figure 5 *ErythroglOSSum lusitanicum*: female plants.

(A–C) Procarp development; supporting cell (sc), sterile cell (stc), carpopogonial branch initial (cbi), cells in carpopogonial branch (cb1, cb2, cb3), and carpopogonium (cp). (D) Habit of female gametophyte; arrows indicate the cystocarps. (E) Cystocarps (arrows). (F) Carposporangia; arrows indicate the synapsis. (G) Cross-section of a cystocarp (G). Scale bars: A–C=20 μ m, D=5 mm, E=1 mm, F=30 μ m, G=200 μ m.

The European Atlantic species of *ErythroglOSSum* are *E. lusitanicum*, *E. laciniatum*, and *E. sandrianum*. The thallus of *E. laciniatum* consists of one or more blades attached directly by a holdfast or by means of a short stipe; blades are branched and fan-shaped to lanceolate; they have macroscopic veins and a variable number of apical cells along apices and margins (Maggs and Hommersand 1993). *E. sandrianum* thalli consist of irregularly branched blades attached by means of a holdfast; blades have lanceolate branches; they develop a midrib and blade growth occurs by means of apical cells located at the apices and margins (Athanasiadis 1985).

The features used by Ardré (1970) for distinguishing between *ErythroglOSSum lusitanicum* and *E. sandrianum* included the presence of stoloniferous branches and the thicker blades in *E. lusitanicum*. We agree with regard to

the first characteristic and we also consider it to be different from *E. laciniatum*. The thallus growth in *E. lusitanicum* is turf-forming, with a basal system composed of entangled stipes and proliferations; this habit differs from the isolated or tufted growth of *E. laciniatum* and *E. sandrianum*. However, we do not consider the thickness of blades as a useful trait for distinguishing between *E. laciniatum* and *E. lusitanicum*, because the ranges of values are overlapping (Table 1). On the other hand, blade thickness can be used for discriminating *E. sandrianum* from the other two species; nevertheless, this characteristic requires further studies, in particular when Ardré (1970) is the only literature source regarding the blade thickness.

The main diagnostic feature of *ErythroglOSSum lusitanicum* is that the growth of blades derives from a single

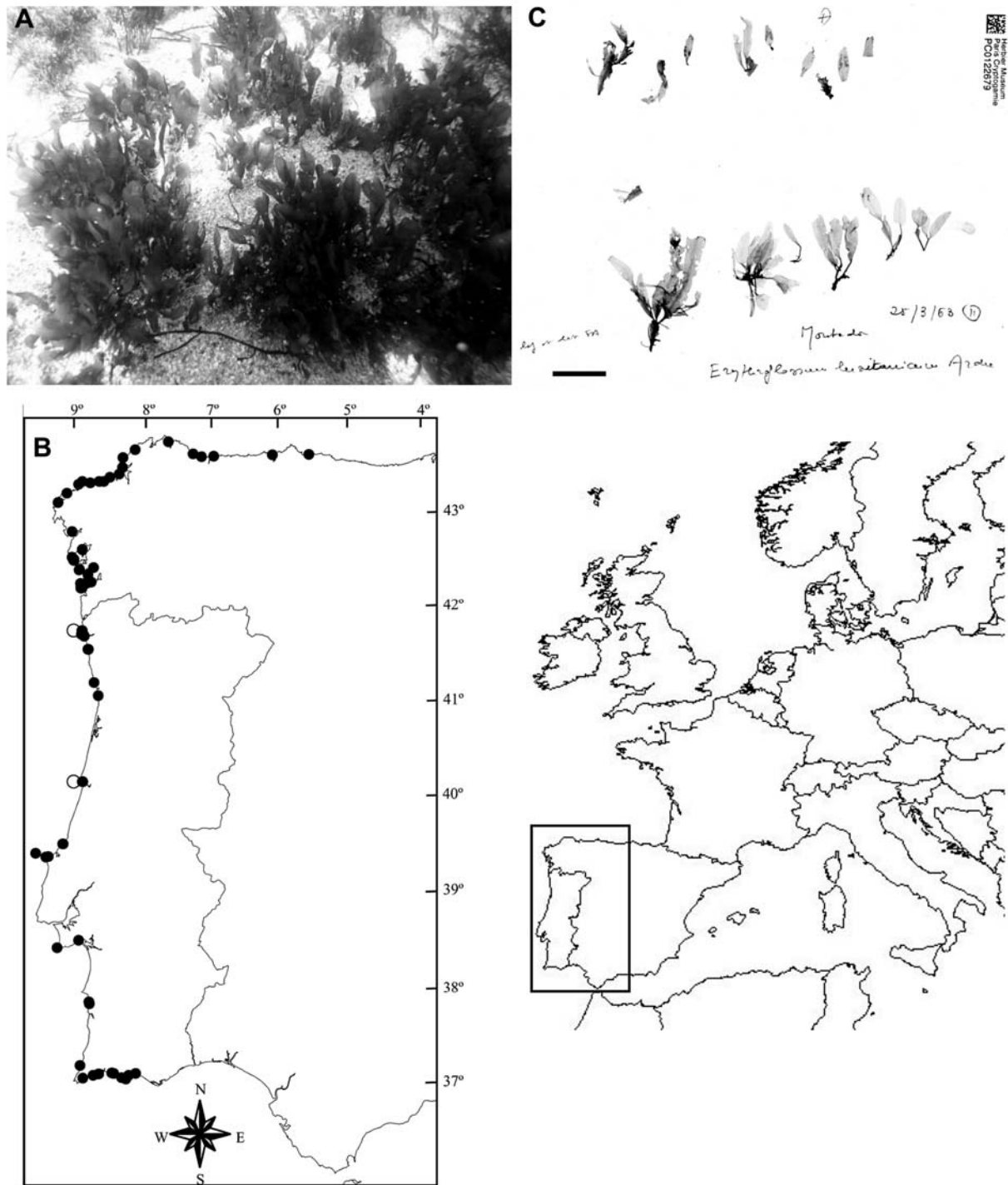


Figure 6 *Erythroglossum lusitanicum*.

(A) Turf; blades ca. 5 cm long. (B) Distribution on the Iberian Peninsula; ○ type localities and ● localities of the later collections. (C) Lectotype of *Erythroglossum lusitanicum*. Scale bar: C=2 cm.

apical cell located in the tip (occasionally 2; fig. 1, pl. 19 in Ardré 1970), while in *E. laciniatum* and *E. sandrianum* it derives from several meristematic cells along apices and margins (Table 1). As a consequence of this type of growth, the blades are simple and ovate-oblongate in *E. lusitanicum*, whereas they are branched and lanceolate in *E. sandrianum* or branched and fan-shaped to lanceolate in *E. laciniatum* (Table 1). Blades have a unique macroscopic vein (midrib) in *E. lusitanicum*, whereas blades in *E. laciniatum* have a network of veins, except

in the narrowest blades where there is a single midrib. Old blades of *E. lusitanicum* sometimes have meristematic cells along broken apices and margins in the basal parts; nevertheless, these cells should be differentiated from the marginal meristematic cells that regularly occur in *E. sandrianum* or *E. laciniatum*. In *E. lusitanicum*, rhizoidal proliferations or new blades with a basal stipe develop as a result of divisions in these marginal meristematic cells, without increasing the size of the blade. In *E. sandrianum* and *E. laciniatum*, marginal meriste-

Table 1 *ErythroGLOSSUM lusitanicum*: comparison of morphological features with other Atlantic European congeners.

	References	Habit	Blade shape and branching	Veins	Number of meristematic cells per blade	Thickness of monostromatic blade areas (µm)	Habitat
<i>ErythroGLOSSUM lusitanicum</i>	2, 7	Turf-forming	Ovate-oblongate; simple	Midrib	1 (2), at the tip	45–75	Sand-influenced bedrock
<i>ErythroGLOSSUM laciniatum</i>	5, 6	Erect	Fan-shaped to lanceolate, branched	Network of veins to midrib in narrowest blades	Several, along apices and margins	50–100	Bedrock
<i>ErythroGLOSSUM sandrianum</i>	1, 2, 3, 4	Erect	Lanceolate, branched	Midrib	Several, along apices and margins	<40	–

References: 1, Kützing (1866); 2, Ardré (1970); 3, Coppejans (1983); 4, Athanasiadis (1985); 5, Maggs and Hommersand (1993); 6, Coppejans (1995); 7, this work.

matic cell activity results in blade expansion or development into branches of the blade. Finally, the typical habitat of *E. lusitanicum* is very specific; the well-developed turfs grow over rocks buried by sand, as pointed out by Ardré (1970), which differs from *E. laciniatum* that grows on bedrock free from the influence of sand (Table 1).

The genus *ErythroGLOSSUM* contains more than 10 species, of which *ErythroGLOSSUM laciniatum*, *E. lusitanicum*, *E. schousboei*, *E. subcostatum*, *E. sandrianum*, and *E. balearicum* J. Agardh ex Kylin are distributed in Europe and North Africa. However, some of these species are poorly known and several synonymies have been suggested: *E. sandrianum* and *E. schousboei* (Athanasiadis 1985), *E. subcostatum* and *E. sandrianum* (Ardré 1970), *E. sandrianum* and *E. laciniatum* (Maggs and Hommersand 1993). Elucidation of the taxonomic status of this species needs to be carried out using a combination of molecular and morphological analysis.

ErythroGLOSSUM lusitanicum is an endemic species from the warm temperate NE Atlantic subregion 1 (van den Hoek and Breeman 1990). At present, the southern limit for *E. lusitanicum* is recorded in Morocco (Benhisoune et al. 2003) and the two localities reported from northern Spain in this work represent its northernmost distribution. The distribution area of *E. lusitanicum* is probably wider, but this species is difficult to detect because it is diminutive. Furthermore, well-developed turfs of *E. lusitanicum* grow in sand-covered rocks in exposed sites, a habitat with a flora that is not well known. These two reasons could explain the lack of collections of *E. lusitanicum* between 1970 and 1995.

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