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Leptofauchea coralligena (Faucheaceae, Rhodophyta), a new species from the Mediterranean Sea

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Morphological and reproductive studies, corroborated by gene sequence data, demonstrate that there are two distinct entities within Mediterranean specimens referable to the red alga *Rhodymenia ardissonei* (Rhodymeniaceae). Genuine *R. ardissonei* grows in shallow water while specimens from deep water habitats, traditionally attributed to the same species, belong to *Leptofauchea*, a genus placed in the Faucheaceae. The deep water growth is herein described as a new species, *Leptofauchea coralligena*. Female gametophytes in *Leptofauchea* are easily distinguished because of the presence of a *tela arachnoidea* in the pericarp cavity and tetrasporangia developing in nemathecia. Sterile specimens, however, can be extremely difficult to tell apart because differences in vegetative morphology and anatomy are subtle. Refractive bodies in the medullary cells form the most conspicuous diagnostic character separating *L. coralligena* from *R. ardissonei*. These structures can be easily observed in young specimens of *L. coralligena*, both in surface view and transverse sections. However this character becomes less obvious or even impossible to observe in mature thalli with medullary cells containing large amounts of floridean starch. Refractive bodies are also difficult to observe in herbarium specimens. The existence of these structures has not previously been reported from any other *Leptofauchea* species. The presence of *L. coralligena* has been confirmed in the western Mediterranean Sea. Atlantic specimens attributed to *R. ardissonei* require further study.

Key words: LSU rDNA, Faucheaceae, *Leptofauchea coralligena*, Mediterranean Sea, reproduction, Rhodymeniales, Rhodophyta, *Rhodymenia ardissonei*, taxonomy

Introduction

Several recent studies dealing with the Rhodophyta or marine diversity in general have highlighted that, in organisms characterized by a limited number of reliable diagnostic characters, the true diversity is likely to be underestimated using a classical morphological–anatomical approach (reviewed in Knowlton, 2000; Brodie & Zuccarello, 2006; Maggs *et al*., 2007). The phenomenon whereby independent evolutionary lineages are attributed to the same taxonomic species, generally referred to as cryptic or pseudocryptic diversity, is probably widespread in the algae and further discoveries of (pseudo-) cryptic species are to be expected. Several studies dealing with European and Mediterranean taxa demonstrate that even along shores which have been studied intensively for over two centuries, our traditional estimates of diversity and knowledge of species boundaries have proved to be inadequate (e.g. De Clerck *et al*., 2005; Saunders & Lehmkuhl, 2005; Brodie *et al*., 2007).

In this study we report on a rhodymenialean species, *Rhodymenia ardissonei* (Kuntze) Feldmann (= *R. corallicola* Ardissone, 1883). This species is common in the Mediterranean Sea from the shallow infralittoral down to the low circalittoral. Despite its considerable ecological range and morphological variation (Feldmann, 1941), the boundaries of the species have hardly been questioned. Ercegovic (1949) distinguished two forms, *R. corallicola* f. *condensata*, for the more compact and shortly segmented shallow water individuals, and f. *expansa* for the more laxly branched individuals from deeper waters. Codomier *et al*. (1988) concluded that the differences between specimens are due only to the type of substratum on which the thallus grows. Based on a comparative study of the morphological development, complemented by ecophysiological experiments, Izquierdo (2003) pointed out that two different entities have been included within this taxon, one living in dark places of the upper infralittoral, usually on sponges

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Table 1. Source of the specimens used in the current molecular analyses. GenBank numbers of newly generated LSU rDNA sequences.

Name	Collection information	Accession number
Gloiocladia spinulosa (Okamura & Segawa) Sánchez & Rodríguez-Prieto	South Africa: Protea Banks, Southern Pinnacle (De Clerck O. & Leliaert F., 9/06/2003, KZN 2217)	EU418772
Lomentaria articulata (Hudson) Lyngbye	Spain: A Coruña, Castillo de San Anton (De Clerck O. & Heytens M., 10/07/2006, ODC 1297)	EU418773
Rhodymenia ardissonei (Kuntze) Feldmann	Spain: Musclera Trencada, Llafranch (Rodríguez-Prieto C., 14/08/2005, ODC 1501)	EU418774
Rhodymenia ardissonei (Kuntze) Feldmann	Spain: Els Corbs, Palamós (Rodríguez-Prieto C., 5/09/2006, ODC 1502)	EU418776
Rhodymenia ardissonei (Kuntze) Feldmann	Spain: Roques Planes, Calonge (Rodríguez-Prieto C., 16/09/2005, ODC 1503)	EU418777
Rhodymenia ardissonei (Kuntze) Feldmann	Spain: Roques Planes, Calonge (Rodríguez-Prieto C., 16/01/2007, ODC 1504)	EU418778
Rhodymenia holmesii Ardissone	France: Nord-Pas de Calais, Audresselles, Pointe du Nid de Corbet (De Clerck O., 16/09/2004, ODC 1019)	EU418775

or epiphytic on *Cystoseira* spp., the other growing on deep substrata, usually on coralline concretions.

Rhodymenia ardissonei is characterized by a flattened, decumbent thallus arising from a discoid holdfast. A stipe can be present or absent and the axes are more-or-less regularly dichotomously branched. The thallus is multiaxial with a solid medulla composed of some layers of large colourless cells, which changes abruptly to an incomplete layer of inner cortical cells and an outer cortex of 1–2 irregular layers of small pigmented cells (Ardissone, 1874 [as *R. corallicola*]; Newton, 1931 [as *R. corallicola*]; Feldmann, 1941; Ercegovic, 1949, 1957, 1963 [as *R. corallicola*]; Ballesteros Sagarra, 1980; Ribera Siguán, 1983; Barceló Martí, 1987; Rull-Lluch, 1987; Codomier *et al.*, 1988; Izquierdo, 2003). Spermatangia were not described, although Rodríguez-Prieto & Polo Albertí (1988) observed them in upper infralittoral specimens. Reproductive information about female reproductive structures and carposporophytes are limited to form, size and location of cystocarps (Ardissone, 1874 [as *R. corallicola*]; Newton, 1931 [as *R. corallicola*]; Codomier *et al.*, 1988). Tetrasporangia are cruciately divided and grouped in sori usually situated in the more distal dichotomies (Ardissone, 1874 [as *R. corallicola*]; Feldmann, 1941; Ballesteros Sagarra, 1980; Codomier *et al.*, 1988).

The lack of information on taxonomically important characters, mainly of the reproductive structures, has hampered our understanding of *R. ardissonei*. Collections of female, male and tetrasporic thalli growing on coralligenous concretions and maërl substrata off the Catalan coast (Spain) by the first author have allowed detailed study of the deep water form. Morphological-anatomical observations indicate a clear distinction between *R. ardissonei* in surface waters and the deep water species, the later representing an undescribed species of *Leptofauchea* Kylin. These results are corroborated by LSU rDNA gene sequences of both species, supplemented with sequences from other Rhodymeniales available in GenBank.

Material and methods

Morphological analyses

Specimens of *Leptofauchea coralligena* were collected by SCUBA from the Mediterranean coasts of Spain, and supplemented with specimens housed at the Herbarium of the University of Girona, Spain (HGI) and Ghent University (GENT HEC). Sections were made with a freezing microtome, and stained either with acidified aqueous 1% aniline-blue and mounted in 50% Karo® corn syrup (Bestfoods, Englewood Cliffs, NJ, USA), or with Wittmann's aceto-iron-haematoxylin-chloral-hydrate and mounted in Hoyer's medium as described in Hommersand *et al.* (1992). Habit photographs were taken with a Canon EOS 350D (Canon, Tokyo, Japan). Photomicrographs were taken with a Spot Insight digital camera (Diagnostic Instruments, Sterling Heights, MI, USA) attached to an Axioskop 2 plus microscope (Zeiss, Berlin, Germany). Voucher specimens and slides were deposited in HGI. Several type and historical collections of Mediterranean *Rhodymenia* species were examined in the course of this study: Ardissone (Università degli Studi di Padova, PAD), Kützing (L), P. & H. Huvé (Centre d'Océanologie de Marseille) and Zanardini (Museo Civico di Storia Naturale, Venezia). Herbarium acronyms follow Holmgren *et al.* (1990).

Molecular analysis

New sequences were generated from samples desiccated in silica gel in the field (Table 1). DNA was extracted, amplified and sequenced as described by Figueroa *et al.* (2007). Amplification of the large subunit rDNA (LSU rDNA) was based on primers and protocols listed in

Harper & Saunders (2001). The newly generated sequences were supplemented by publicly available LSU sequences, selected to ensure as complete a representation as possible of the Rhodymeniales. These sequences were previously published by Harper & Saunders (2001), Le Gall & Saunders (2006), Saunders *et al*. (2006), Withall & Saunders (2006), Ballantine *et al*. (2007) and Dalen & Saunders (2007). Sequences were aligned using MAFFT v.5.3 as described by Katoh *et al*. (2005). The alignment was exported to PAUP 4.0b10 (Swofford, 2002) for maximum likelihood analyses (ML), and MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) for Bayesian inference (BI). A combination of sequences of related orders, Halymeniales, Nemastomatales and Sebdeniales were selected as outgroup taxa. The nucleotide substitution model for ML was selected with Modeltest 3.7 (Posada & Crandall, 1998) according to the Akaike Information Criterion (Posada & Buckley, 2004). Maximum likelihood analyses consisted of heuristic searches with 1000 random sequence addition replicates and TBR with the option MULTREES in effect. Bootstrap analyses consisted of 500 replications of heuristic searches with the number of rearrangements limited to 10,000 (or 3, 600 seconds) for each replicate, using a neighbour joining tree as starting tree. Bayesian analyses were performed using a $GTR + I + \Gamma$ model. The dataset was divided in two, corresponding to the first plus second and the third codon positions with all model parameters uncoupled between the partitions. Posterior probabilities were estimated using a Metropolis-coupled Markov chain Monte Carlo approach sampled according to the Metropolis-Hastings algorithm. The analysis used four chains, one cold and three incrementally heated. Each run consisted of 2×10^6 generations and was sampled every 1000 generations. Burnin values were set at 500,000 generations.

Observations

Species description

***Leptofauchea coralligena* sp. nov**.

Thallus compressus, complanatus, dichotome vel irregulariter ramificatus, 5–6 (−9) cm altus, 4 (−6) mm latus et 75–180 μm crassus; stipes in plantis iuvenilibus tantum distinctus. Medulla 2–4-stratosa; cortex extimus 1–2-stratosus. Cellulae medullares corpora sphaerica rifrangentia, 4–16 μm lata, includentes. Cystocarpia substipitata et globosa, in marginibus tantum praesentia. Nemathecia tetrasporangifera in segmentis subterminalibus, e superficie laminae protrudentes.

Thallus flattened, complanate, dichotomous to irregularly branched, up to 5–6 (−9) cm high, 4 (−6) mm wide and 75–180 μm thick; stipe only distinct in young specimens. Medulla 2–4 layered; outer cortex 1–2 layered. Medullary cells with spherical refractive bodies, 4–16 μm in diameter. Cystocarps substipitate and globose, restricted to the margins. Tetrasporangial nemathecia in subterminal segments on both surfaces of the blade.

HOLOTYPE: HGI-A 7857, a female gametophyte collected by C. Rodríguez-Prieto, 28 September 2003, at −38 m (Fig. 1).

TYPE LOCALITY: Formigues Islands, Palamós, Spain.

DISTRIBUTION: Known with certainty only from the Western Mediterranean Sea.

ETYMOLOGY: Named for the ecology of the species which most typically grows on coralligenous concretions.

HABITAT: *Leptofauchea coralligena* grows in the deep infralittoral and in the circalittoral, mostly between 25 and 75 m deep, on rocky bottoms or coralline concretions, where it can be extremely abundant. Occasionally the species is collected from maërl.

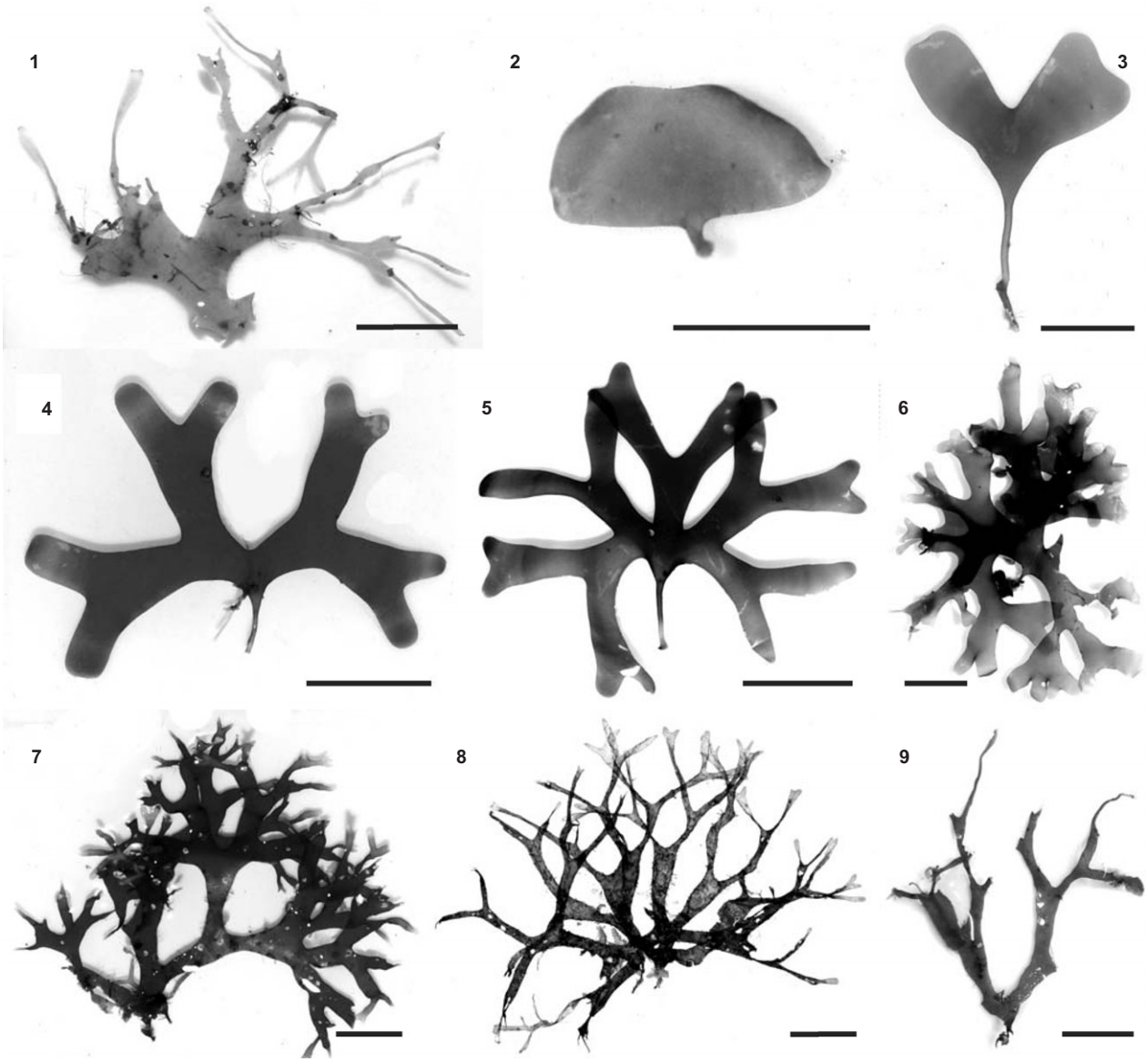
SEASONALITY: Spermatangia were observed in March, cystocarps occur from June to October, and tetrasporangia were found from May to October.

OTHER SPECIMENS EXAMINED: **Spain**: Cap de Creus (E. Ballesteros, 20 June 1996, −30 to 35 m, HGI-A 1930 ♀); El Cairo, Palamós (C. Rodríguez-Prieto, 1 May 2006, −30 m, HGI-A 7468; 5 May 2007, −35 m, HGI-A 7333; 27 January 2007, −30 m, HGI-A 7464); Formigues Islands, Palamós (C. Rodríguez-Prieto, 27 June 1999, −30 m, HGI-A 6472 ♀; 12 August 2001, −38 m, HGI-A 5702; 17 March 2002, −32 m, HGI-A 5720 ♂; 16 June 2002, −30 m, HGI-A 5726 ⊕; 27 October 2002, −31 m, HGI-A 5731 ⊕, HGI-A 7626 ♀; 7 September 2003, −45 m, HGI-A 5922; 28 September 2003, −38 m, HGI-A 6095 ♀; 3 October 2004, −37 m, HGI-A 7470; 3 April 2006, −35 m, HGI-A 7466, HGI-A 7467; 2 July 2006, −37 m, HGI-A 7469; 4 March 2007, −35 m, HGI-A 7465); La Llosa, Palamós (C. Rodríguez-Prieto, 14 May 1997; −36 m; HGI-A 1924 ⊕); La Roja, Platja d'Aro (A. Clavell, 6 April 1997, −30 m, HGI-A 1927); Medes Islands, L'Estartit (C. Rodríguez-Prieto, 24 August 2001, −25 m, HGI-A 5703); Ses Negres, Begur (C. Rodríguez-Prieto, 3 August 1999, −30 m, HGI-A 2335 ♀). **France:** Cap l'Abeille, Banyuls-sur-Mer (E. Coppejans, 12 August 1974, −25 m, GENT HEC 2176 ⊕); Roches Torreilles, Banyuls-sur-Mer (E. Coppejans, July 1974, dredged at −40 to 50 m, GENT HEC 2558; 23 August 1978, GENT HEC 3764; 9 August 1979, −35 m, GENT HEC 4135); Cap Oullestreil, Banyuls-sur-Mer (E. Coppejans, 13 August 1976, −25 m, GENT HEC 2586; 18 August 1978, −20 m, GENT HEC 3759). **Corsica:** Sec de Centuri, Cap Corse, (E. Coppejans, 25 July 1983, –51 m, GENT HEC 5336); Palazzino (E. Ballesteros, 13 October 2005, HGI-A 6985 ♀); Baie de Calvi (E. Coppejans, 8

September 1978, −75 m, GENT HEC 3839); La Revellata, Calvi (E. Coppejans, August 1983, −35 m, GENT HEC 5453).

Habit and vegetative structure

Leptofauchea coralligena is an annual species that undergoes considerable morphological change as it develops. In winter (January), small, flabellate thalli with short stipes grow from discrete holdfasts (Fig. 2). These thalli gradually divide dichotomously in a regular manner until the end of spring, giving rise to erect, flattened, complanate fronds, 4 (−6) mm wide, with rounded, furcate apices and smooth margins (Figs 3–6). In early summer the morphology changes considerably. Thalli become less regularly branched and proliferous from the margin, reaching a height of 5–6 (−9) cm (Fig. 7). At the end of the growth season, late summer and autumn, thalli degrade, lose a considerable portion of their branches and most of the remaining terminal apices become filiform (Figs 8–9). Thalli are first attached to the substratum by a discoid holdfast, which gives rise to a distinctive cartilaginous, terete stipe, up to 1.5 mm long and 1 mm in diameter (Figs 2–6). Especially from summer onwards, plants may attach by secondary marginal haptera and become decumbent, imbricate and anastomosing (Figs 7–8). Occasionally, the primary point of attachment and stipe are lost (Fig. 1). Thalli are 75–180 μm thick, cartilaginous, bright rose, reddish, or occasionally whitish in adult specimens.



Figs 1–9. Habit of the holotype of *Leptofauchea coralligena* and some sterile specimens at different times of the year. Fig. 1. Holotype. A female specimen (HGI-7857). Fig. 2. January (HGI-7464). Fig. 3. March (HGI-7465). Figs 4–5. April (HGI-7466, 7467). Fig. 6. May (HGI-7468). Fig. 7. July (HGI-7469). Fig. 8. August (GENT HEC-2176). Fig. 9. October (HGI-7470). Scale bars: 1 cm (Figs 1, 4–9); 0.5 cm (Figs 2–3)

Axes are multiaxial and solid, initiated from many transversely divided apical cells, with large medullary cells that switch quite abruptly in size to the inner cortical cells. The cortex is composed of 1–2 layers of small, pigmented cells, ovoid or rounded in cross section (Fig. 10), isodiametric to elongated in longitudinal section (Fig. 11), diminishing in size towards the exterior (inner cells 18–30 × 6–13 μm in surface view; outer cells 6–9 × 5–7 μm in surface view), and without lateral secondary pit-connections (Figs 10–13). The medulla is composed of 2–4 layers of large, hyaline cells, ovoid or rounded in transverse section (Fig. 10) and elongated in longitudinal section (Fig. 11). As a general rule medullary cells diminish in size towards the periphery, and are up to 12–60 × 12–55 μm in transverse section and 45–185 × 30–65 μm in longitudinal section. However, in surface view it becomes clear that even the large cells of the central medullary layers are interspersed with distinctively smaller cells (Figs 18–19). Irrespective of size, many medullary cells have lenticular cell wall thickenings (Figs 10–11, 14). Multicellular rhizoidal filaments are very occasionally present in the basal parts of adult thalli, developing from inner cortical cells or outer medullary cells, and growing between the medullary cells (Fig. 15). Cells of rhizoidal filaments are rectangular to ovoid, 20–45 × 8–20 μm, connected to the nearby medullary cells by secondary pit-connections. Groups of ovoid to rounded secondary medullary cells, 15–28 × 13–21 μm, are also very occasionally present in the basal parts of adult specimens. They are interspersed among the large medullary cells (Fig. 16).

One to few spherical refractive bodies, 4–16 μm in diameter, may be present in medullary cells appressed to the inner wall of the cells (Fig. 17). The occurrence of refractive bodies varies both within the different parts of the thallus and with the age of the specimen. They are most common and conspicuous in young specimens where they can be easily observed in surface view (Fig. 18). Later in the season the frequency of cells with refractive bodies diminishes in the thallus. Furthermore, they become more difficult to observe due to the accumulation of large amounts of floridean starch in the medullary cells (Fig. 19).

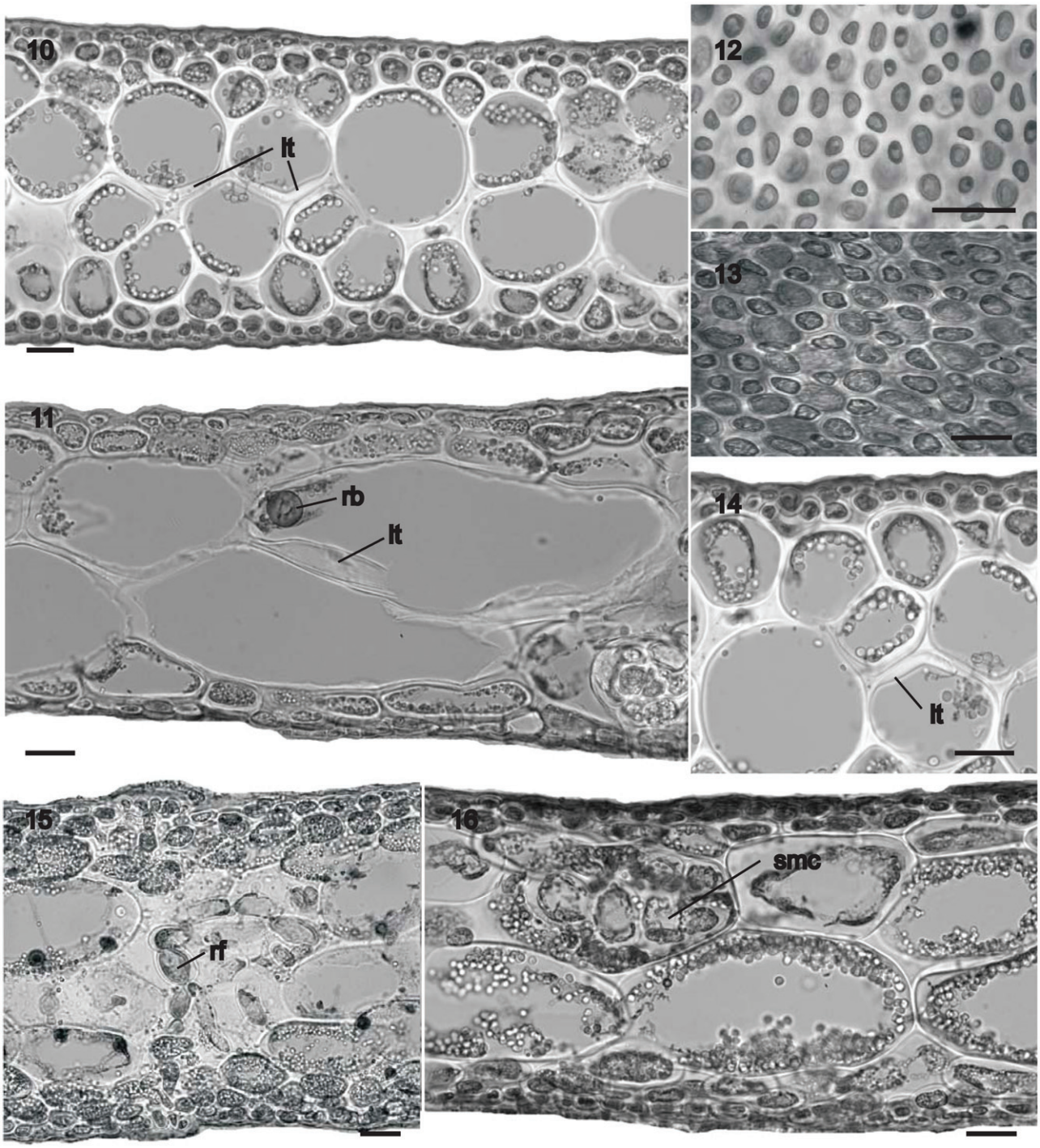
The stipe is composed of rounded or ovoid medullary cells which are smaller than in the rest of the frond (up to 60 μm in diameter), and which also bear refractive bodies (Figs 20–21).

Reproductive structures

Plants are monoecious. Spermatangia, ca. 2 μm in diameter, are grouped in surface sori situated in the apical parts of the branches, and cut off singly from ovoid spermatangial mother cells that develop from the outer cortical cells (Figs 22–25). Female gametophytes form procarps with a curved, three-celled, outwardly directly carpogonial branch. The supporting cell is a peripheral medullary cell which is conspicuously enlarged (Fig. 26). The young auxiliary cell branch was not observed. Mature auxiliary cell branches are two-celled, composed of an auxiliary mother cell and a terminal auxiliary cell (Figs 27–28). Diploidization of the auxiliary cell was not observed. A transverse division of the latter gives rise to the primary gonimoblast cell (= gonimoblast initial) (Figs 27–28). A fusion cell is formed by enlargement of the pit-connection between the auxiliary cell and the auxiliary mother cell. Components of the fusion cell become indiscernible when the structure is mature (Figs 29–30). The gonimoblast (up to 280 μm in diameter) arises from the distal end of the primary gonimoblast cell and is composed of several elongated lobes of ovoid carposporangia (Figs 29–30). Most cells of the gonimoblast develop into carposporangia, 7–13 μm in diameter (Fig. 31), but a sparingly branched framework of multinucleate sterile cells remains (Fig. 32). Cystocarps (up to 750 μm in diameter) are situated on the branch margins, substipitate, globose and ostiolate (Fig. 33).

Coinciding with the development of the procarp and the early post-fertilisation stages, the underlying and neighbouring medullary cells start to transform (Fig. 34) and pericarp development is initiated. Peripheral medullary cells become stretched (Fig. 34) and form a persistent network of filaments (=*tela arachnoidea*) that surrounds the procarp (Figs 34–35). Cells of the *tela arachnoidea* are stellate, 11–23 μm in diameter with lobes up to 18 μm long (Figs 29–30, 34–36), characterized by a distinctive refractive body, identical to the one seen in medullary cells (Fig. 36). The upper region of the mature cystocarp lacks the typical, small-celled cortex of the vegetative region and is composed of distal compacted cells of the *tela arachnoidea* (Figs 37–38). For this reason they also present a distinctive refractive body (Fig. 37).

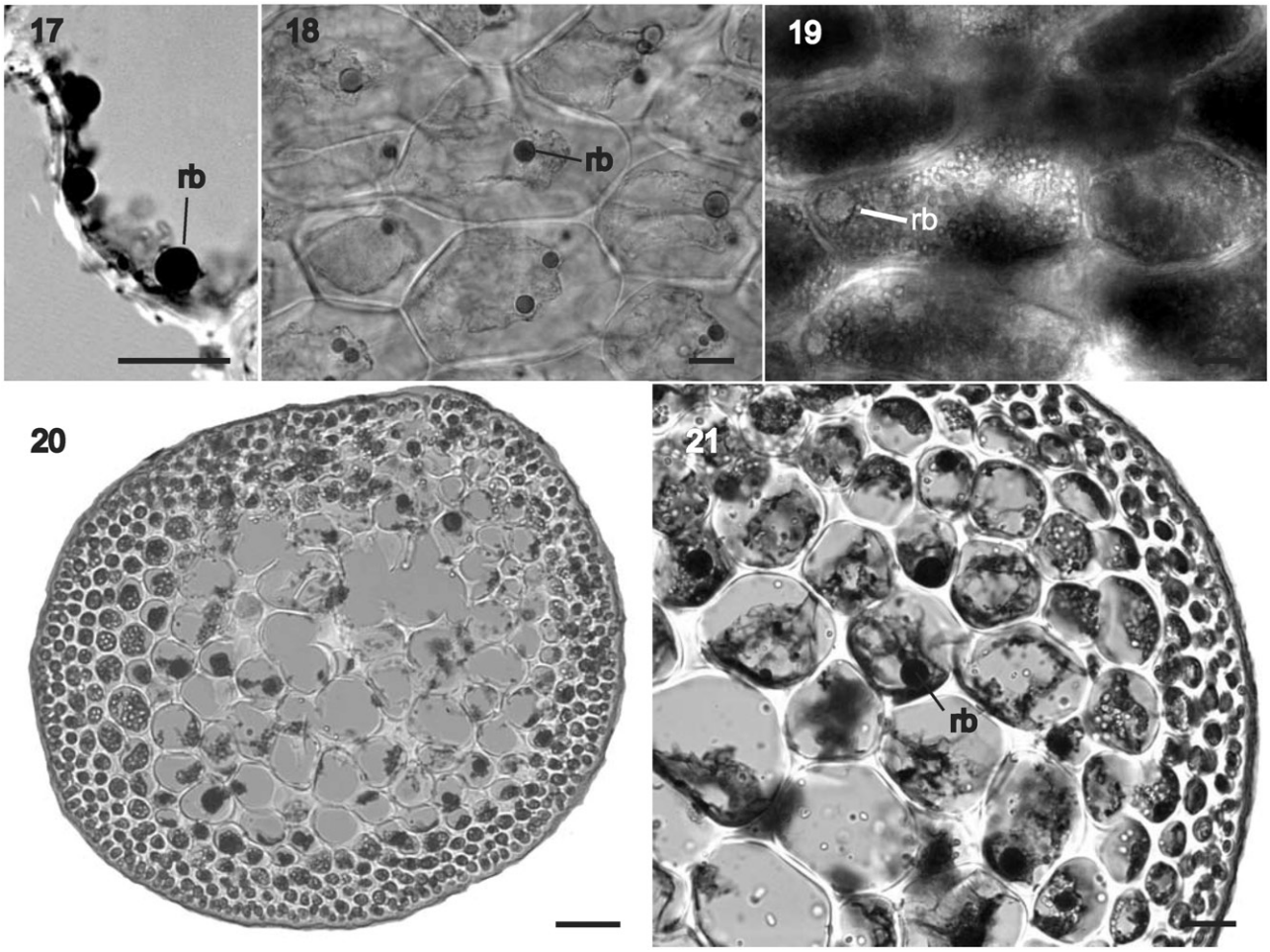
After fertilization, cells surrounding the supporting cell develop into a subspherical mass of darkly staining, multinucleate nutritive cells, connected to each other and to the supporting cell by secondary pit-connections. These cells are somewhat stellate, with the main cell body 9–16 μm in diameter and lobes up to 2 μm long (Figs 29–30, 35, 38). As the gonimoblast matures it gradually fills the entire pericarp cavity, pushing the cells of the *tela arachnoidea* to the outer periphery. Likewise, the stellate cells subtending the nutritive tissue become compressed and as a consequence it appears as



Figs 10–16. Vegetative structure of *Leptofauchea coralligena* stained with aniline blue. Figs 10–11. Transverse (Fig. 10) and longitudinal (Fig. 11) sections of the middle part of the plant (HGI-A 7626, 5702). Fig. 12. Outer cortical cells in surface view (HGI-A 6472). Fig. 13. Inner cortical cells in surface view (HGI-A 6095). Fig. 14. Detail of the lenticular thickness of medullary cells in cross section (HGI-A 7626). Fig. 15. Transverse section of the basal part of the thallus showing the development of rhizoidal filaments (HGI-A 6472). Fig. 16. Transverse section of the basal part of the thallus with many secondary medullary cells (HGI-A 7626). Abbreviations: lt: lenticular thickening; rb: refractive body; rf: rhizoidal filament; smc: secondary medullary cell. Scale bars: 20 μm

though the nutritive tissue is in contact with the ordinary medullary cells (Fig. 38).

Tetrasporangia develop in ovoid to elongate nemathecia situated in the middle part of the branch tips (Fig. 39) and are prominent on both sides of the blade (Fig. 40). Paraphyseal filaments are up to 7–8 (−9) cells long, and tetrasporangia are ovoid or fusiform, measuring 35–60 × 20–40 μm, decussate cruciate, or, occasionally, cruciate or irregular (Figs 41–43). Tetrasporangia are cut off laterally from one of the first dichotomies of a nemathecial filament, with the



Figs 17–21. Vegetative structure of *Leptofauchea coralligena* stained with aniline blue. Fig. 17. Detail of refractive bodies (HGI-A 7333). Figs 18–19. Surface view of the apex of a young (Fig. 18) and an old (Fig. 19) specimen. The refractive bodies are easily distinguishable in the younger, but are obscured by abundant floridean starch in the older (HGI-A 1927, 5922). Figs 20–21. Transverse sections of the stipe (HGI-A 5703, 7333). Abbreviation: rb: refractive body. Scale bars: 20 μm

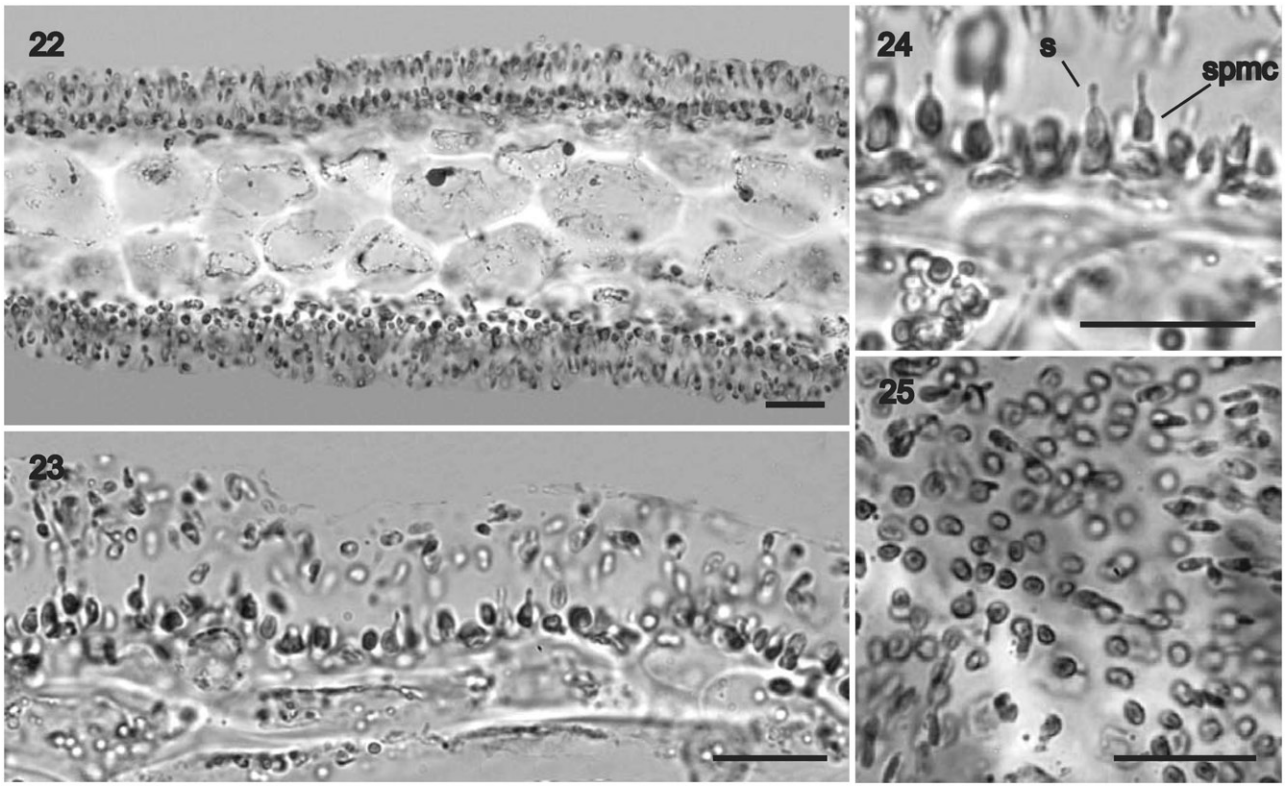
pit-connection between the tetrasporangium and the filament situated laterally, but very close to the basal part of the tetrasporangium.

Notes

The white colour of some adult specimens of *L. coralligena* could be due to the accumulation of floridean starch, as seen in other Rhodophyta such as *Gloiocladia repens* (C. Agardh) Sánchez et Rodríguez-Prieto (Rodríguez-Prieto *et al*., 2007) or *Kallymenia feldmannii* Codomier and *K. requienii* (J. Agardh) J. Agardh (Rodríguez-Prieto & Vergés, 2001). Rhizoidal filaments and secondary medullary cells are correlated with injury of the thallus (Sparling, 1957; Irvine & Guiry, 1980; Sánchez, 2005; Sánchez & Rodríguez-Prieto, 2005; Rodríguez-Prieto *et al*., 2007) and could be involved in increasing thallus toughness (Sánchez, 2005; Sánchez & Rodríguez-Prieto, 2005; Rodríguez-Prieto *et al*., 2007).

Molecular analyses

The molecular data set consisted of 38 LSU rDNA sequences of Rhodymeniales. Three species belonging to the most closely related orders were selected as outgroups: *Sebdenia flabellata* (Sebdeniales), *Pachymenia carnosa* (Halymeniales) and *Tsengia laingii* (Nemastomatales). From the alignment with a total length of 3075 characters, 294 ambiguously aligned positions were excluded for the ML and BI. Figure 44 presents the maximum likelihood tree. Bayesian inference produced a set of trees of similar topology. The currently accepted rhodymenialean families (Champiaceae, Faucheaceae, Lomentariaceae and Rhodymeniaceae) as well as a thus far undescribed lineage containing *Asteromenia* Huisman & Millar, *Erythrymenia* Schmitz ex Mazza and *Hymenocladia* J. Agardh emerge as well-supported clades receiving a 100% support in BI and ML analyses. *Rhodymenia ardissonei*, the species from shallow waters, is resolved as a monophyletic lineage sister to *R. holmesii* Ardissone and



Figs 22–25. Light photomicrographs of male reproductive structures of *Leptofauchea coralligena* stained with aniline blue. Figs 22–23. Transverse sections of a fertile area of the thallus showing a spermatangial sori (HGI-A 5720). Fig. 24. Transverse section of a fertile area of the thallus showing spermatia borne on spermatangial mother cells (HGI-A 5720). Fig. 25. Detail of a spermatangial sorus in surface view (HGI-A 5720). Abbreviations: s: spermatium; spmc: spermatangial mother cell. Scale bars: 20 μm

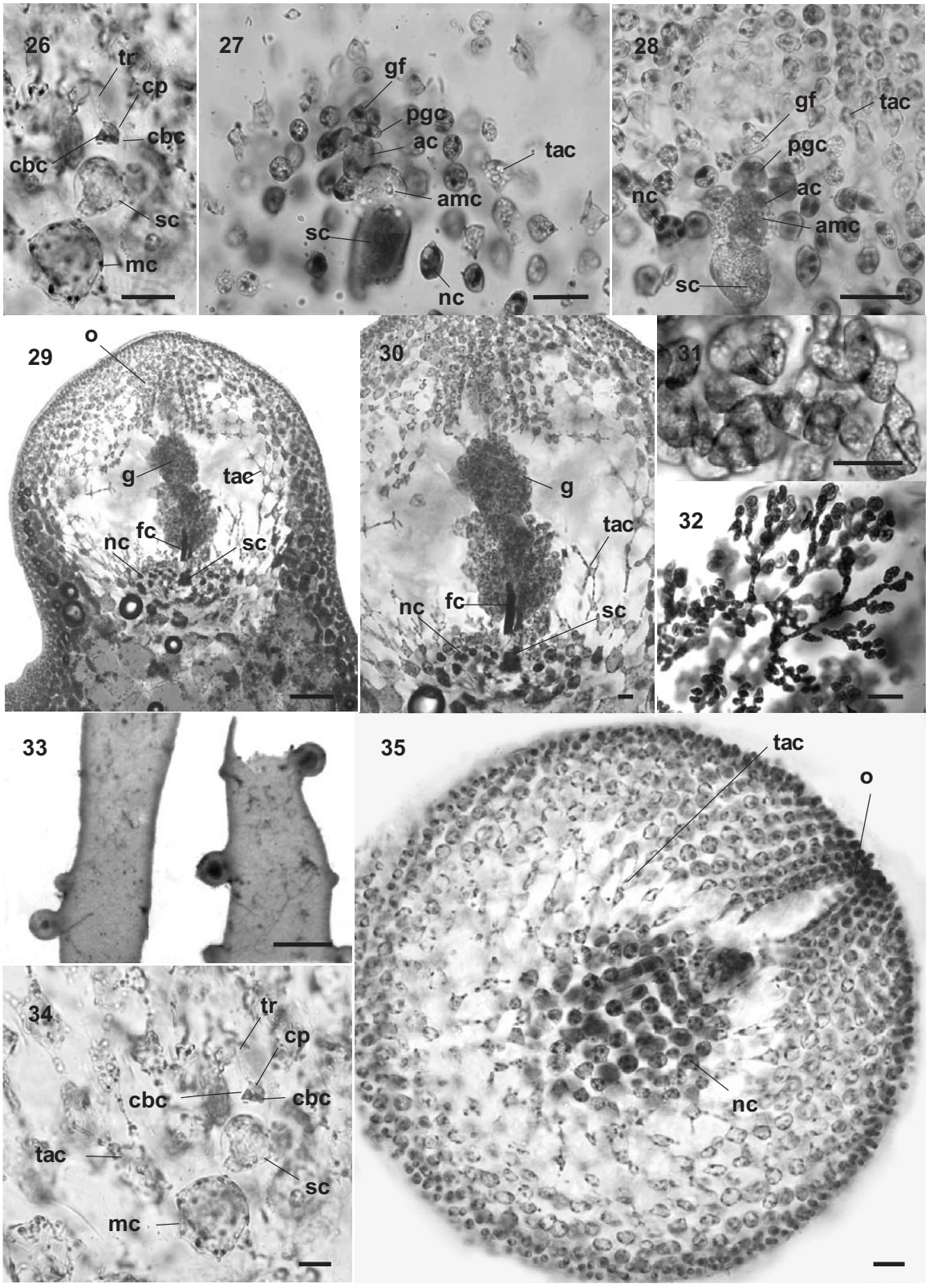
Cordylecladia erecta (Greville) J. Agardh. *Leptofauchea coralligena* grouped with *L. pacifica* E.Y. Dawson, *L. chiloensis* Dalen & G.W. Saunders and an undescribed *Leptofauchea* species from Western Australia. The genus *Leptofauchea* was resolved as the sister taxon of *Webervanbossea* G. De Toni in the Faucheaceae which also contains *Gloioderma* J. Agardh and *Gloiocladia* J. Agardh.

Observations and nomenclature of Mediterranean Rhodymenia *species*

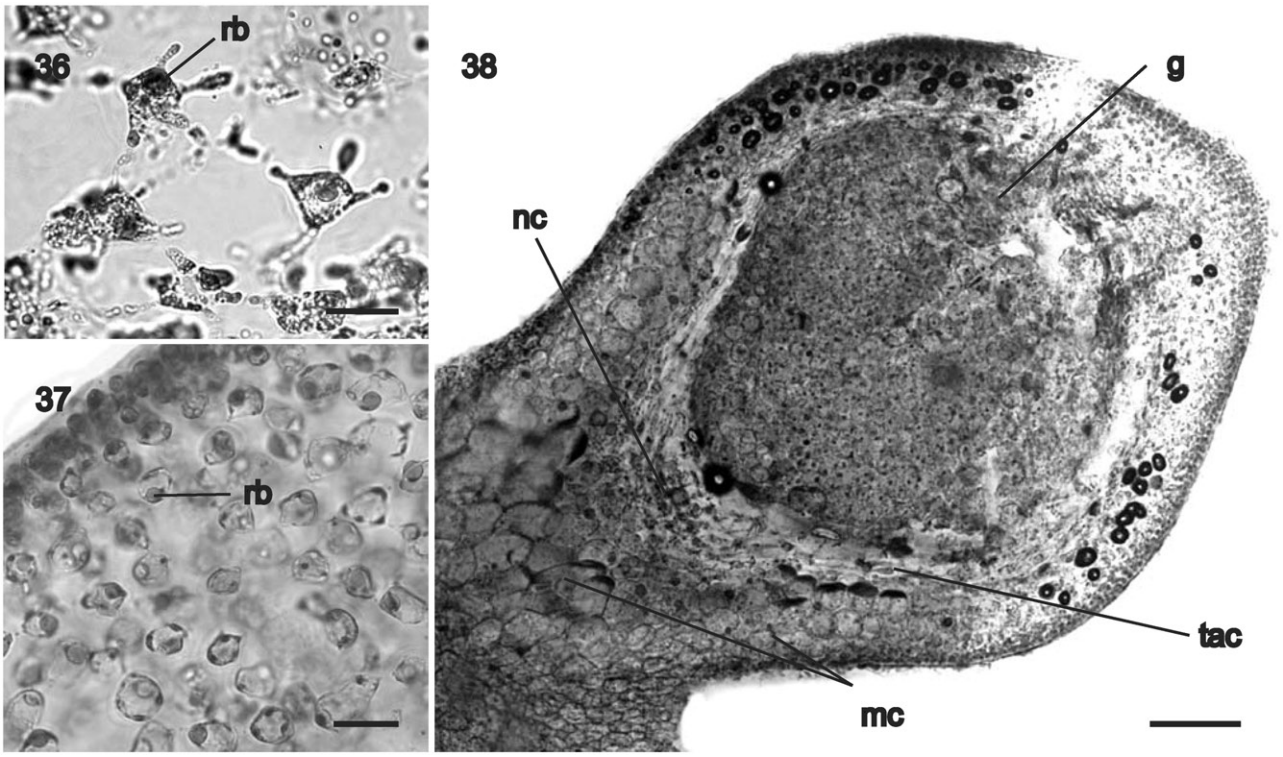
Because of the historical confusion of the recently described *L. coralligena* with *R. ardissonei*, the type collection of the latter species was examined to ascertain its identity. In addition, the type specimen of *R. ligulata* Zanardini, a species described from the Adriatic and treated as a synonym of *R. corallicola* by several authors (e.g. Funk, 1927), was examined.

Rhodymenia ardissonei was validly described as *R. corallicola* (Ardissone, 1883) from Porto Maurizio, Italy. This name, however, is illegitimate, being a later homonym of *R. corallicola* (Zanardini) Ardissone (1874), a name based on *Gracilaria corallicola* Zanardini (1843). The latter species is still considered a *Gracilaria* species (see Feldmann, 1941). It should be noted, however, that both the description and illustration by Ardissone (1874, pl. 9) are of a *Rhodymenia*, rather than a *Gracilaria* species. Independently and coincidentally both Kuntze (1891) and Feldmann (1937) used the same epithet for *Palmaria ardissonei* Kuntze and *R. ardissonei* Feldmann, respectively. If treated as independent names, *R. ardissonei* Feldmann is superfluous and hence illegitimate. Therefore, Feldmann's name was treated as a new combination, *R. ardissonei* (Kuntze) Feldmann.

In PAD all specimens filed under the number 1937 clearly belong to *R. ardissonei*, except one, which is a Delesseriaceae. A single specimen corresponds to the protologue of *R. corallicola* Ardissone and is considered the holotype: PAD 1937, Porto Maurizio, Italy, August 1875; Dall alto mare (Fig. 45). The specimen corresponds to the concept of *R. ardissonei* from shaded, shallow environments. It resembles *L. coralligena*, but the branching pattern is somewhat less regular, apices are not filiform and medullary cells lack refractive bodies. In addition Ardissone's illustrations (1874: pl. 9) are indicative of a *Rhodymenia* rather than *Leptofauchea* due to the absence of a *tela arachnoidea* in the mature cystocarp cavity and the presence



Figs 26–35. Light photomicrographs of female reproductive structures and postfertilization stages of *Leptofauchea coralligena*. Fig. 26. Carpogonial branch, haematoxylin stained (HGI-A 6985). Fig. 27. Young gonimoblast arising from the primary gonimoblast cell (HGI-A 6472). Fig. 28. Detail of a mature procarp where multinucleated stellate nutritive cells can be distinguished, haematoxylin stained (HGI-A 6472). Figs 29–30. General view and detail of a mature cystocarp, aniline blue stained (HGI-A 1930). Fig. 31. Carpospores, haematoxylin stained (HGI-A 6472). Fig. 32. Sparingly branched framework of multinucleate sterile cells remaining within the mature gonimoblast, aniline blue stained (HGI-A 6985). Fig. 33. Cystocarps on the thallus (HGI-A 2335). Fig. 34. Procarp development, haematoxylin stained (HGI-A 6985). Fig. 35. General view of a young carposporophyte with the spherical mass of nutritive cells, haematoxylin stained (HGI-A 6472). Abbreviations: ac: auxiliary cell; amc: auxiliary mother cell; cbc: carpogonial branch cell; cp: carpogonium; fc: fusion cell; g: gonimoblast; mc: medullary cell; nc: nutritive cell; pgc: primary gonimoblast cell; sc: supporting cell; tr: trichogyne; tac: cell of the *tela arachnoidea*. Scale bars: 20 μm (Figs 26–28, 30, 32, 34–35); 100 μm (Fig. 29); 50 μm (Fig. 31); 1,000 μm (Fig. 33)



Figs 36–38. Light photomicrographs of postfertilization stages of *Leptofauchea coralligena*. Fig. 36. Detail of stellate cells of the *tela arachnoidea*, where refractive bodies are well distinguishable, aniline blue stained (HGI-A 6472). Fig. 37. Detail of the marginal cells of the upper part of a cystocarp, connected to neighbouring cells by many pit-connection. Just like cells of the *tela arachnoidea* each cell has a refractive body, haematoxylin stained (HGI-A 6472). Fig. 38. Mature cystocarp, the gonimoblast filling the cystocarp cavity, with nutritive tissue compressed at the bottom of the cavity, *tela arachnoidea* being compressed to the margin of the cavity, and ordinary medullary cells are present only in the middle part of the cystocarp, haematoxylin stained (HGI-A 6093). Abbreviations: g: gonimoblast; mc: medullary cell; nc: nutritive cell; rb: refractive body; tac: cell of the *tela arachnoidea*. Scale bars: 20 μm (Figs 36–37); 100 μm (Fig. 38)

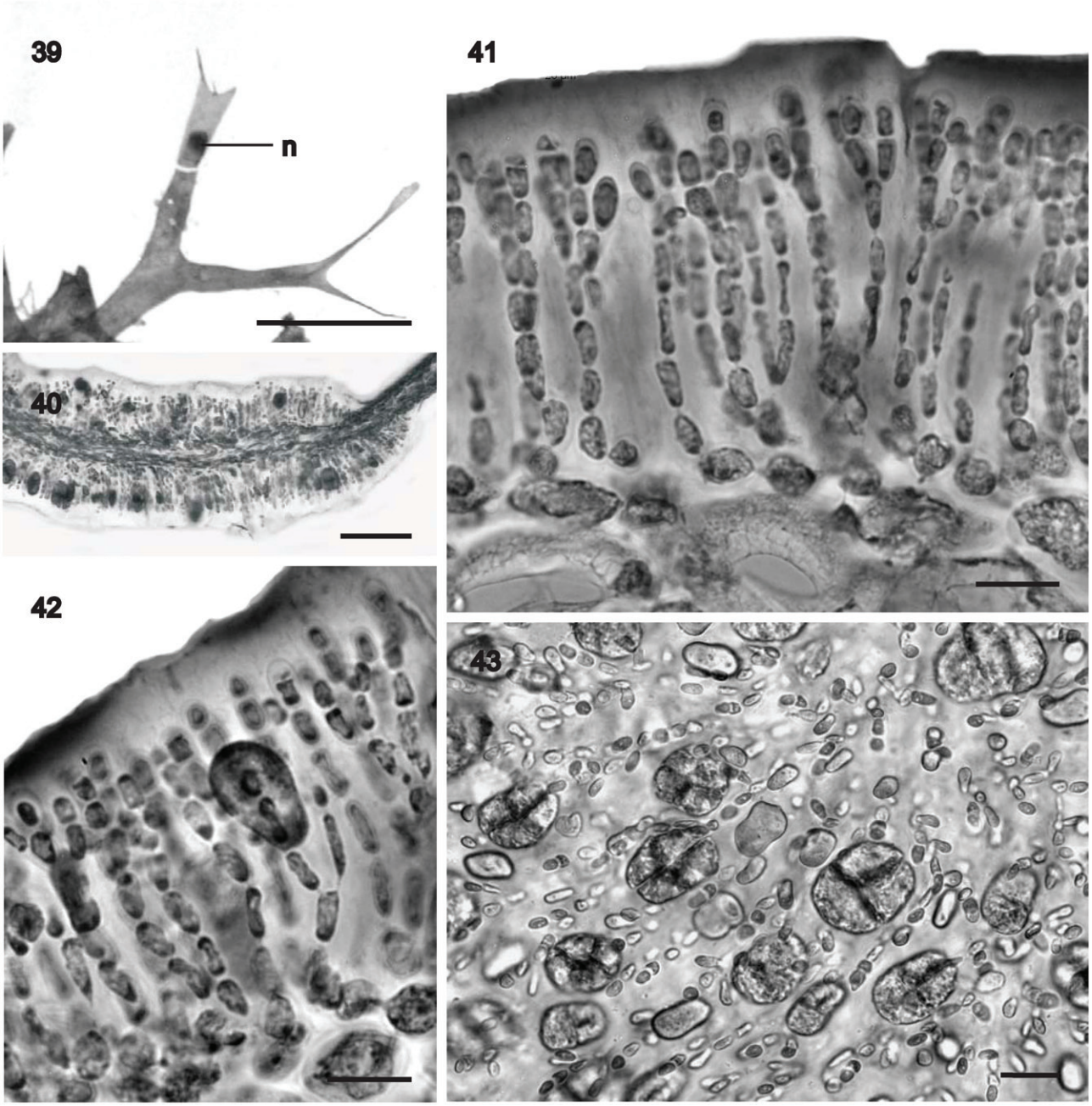
of tetrasporangia that are embedded in an undifferentiated cortex rather than nemathecia.

A description of *Rhodymenia ligulata* Zanardini was not provided (Zanardini, 1843), but the name is validated by reference to a description of the species in Meneghini (1842). The name served as the basionym of both *Sphaerococcus ligulatus* (Zanardini) Kützing (1845) and *Palmaria ligulata* (Zanardini) Kuntze (1891). Since, *Sphaerococcus meneghini* Kützing (1849) is explicitly based on Meneghini's unnamed species, it is an illegitimate superfluous name. The Meneghini specimen from Dalmatia is housed in the Kützing herbarium (L 0650250, Fig. 46) and was depicted by Kützing in his Tabulae Phycologicae (Kützing, 1868: 33, pl. 96*a*, *b*). *Rhodymenia ligulata* appears to be a very different species from *R. ardissonei*, characterized by branches up to 6 (−7) mm wide and ligulate apices which do not become filiform in worn specimens, margins irregularly dentate to ciliate and medullary cells lacking refractive bodies.

Discussion

During the last decade the classification of the Rhodymeniales has been refined considerably at every taxonomic level (Saunders *et al.* 1999, 2006; Dalen & Saunders, 2007; Rodríguez-Prieto *et al.*, 2007). Gene sequences indicated that general morphology and vegetative anatomy often provide inadequate estimates of diversity. Not only is cryptic diversity rife in red algal genera, it is also particularly hard to assign species to the correct genus or even family in the absence of reproductive structures, mainly those of the female gametophytes. In the present paper we demonstrate that two distinct entities are included within *R. ardissonei*, genuine *R. ardissonei* and the presently described *L. coralligena*. Furthermore, these species belong to two well-differentiated families, Rhodymeniaceae and Faucheaceae respectively. Differences between the genera are restricted to reproductive structures. Gene sequence data confirms our morphological results by resolving *R. ardissonei* as the sister taxon of *R. holmesii* and *Cordylecladia erecta*, whereas *Leptofauchea coralligena* clusters with *Leptofauchea* in the Faucheaceae.

The genus *Leptofauchea*, described by Kylin (1931), presently includes four species which are widely distributed throughout the world's oceans: the type species *L. nitophylloides* (J. Agardh) Kylin



Figs 39–43. Tetrasporangial development in *Leptofauchea coralligena*, aniline blue stained. Fig. 39. Nemathecium in surface view (GENT HEC 2176). Fig. 40. Transverse section of a nemathecium (GENT HEC 2176). Figs 41–42. Detail of the nemathecial filaments (HGI-A 5731). Fig. 43. Detail of the nemathecium in surface view (GENT HEC 2176). Abbreviation: *n*: nemathecium. Scale bars: 1 cm (Fig. 39); 100 µm (Fig. 40); 20 µm (Figs 41–43).

from Australia, *L. rhodymenioides* W.R. Taylor from the Caribbean Sea, *L. pacifica* E.Y. Dawson from the eastern Pacific and *L. chiloensis* Dalen & G.W. Saunders from Chile (Dalen & Saunders, 2007). A few more species currently assigned to *Leptofauchea* are insufficiently known to allow unequivocal placement. *Leptofauchea coralligena* is the first record of the genus in the Mediterranean Sea. The genus is characterized by a medulla of several layers of cells grading abruptly in size to a thin cortical layer, smooth, ostiolate cystocarps with a well-defined *tela arachnoidea*, and tetrasporangia forming in nemathecial sori on a single blade surface (Dalen & Saunders, 2007). Despite the fact that the taxonomic value of the latter structure was criticised by Sparling (1957), it appears to be a well-defined character which unites the genera of the Faucheaceae. However, in *Webervanbossea*, the network of stretched cells is not well-developed (Huisman, 1995).

Our observations allow a clear view of the ontogeny of the *tela arachnoidea* in *Leptofauchea*. During procarp development medullary cells surrounding the supporting cell start to divide and differentiate. Cells gradually stretch and

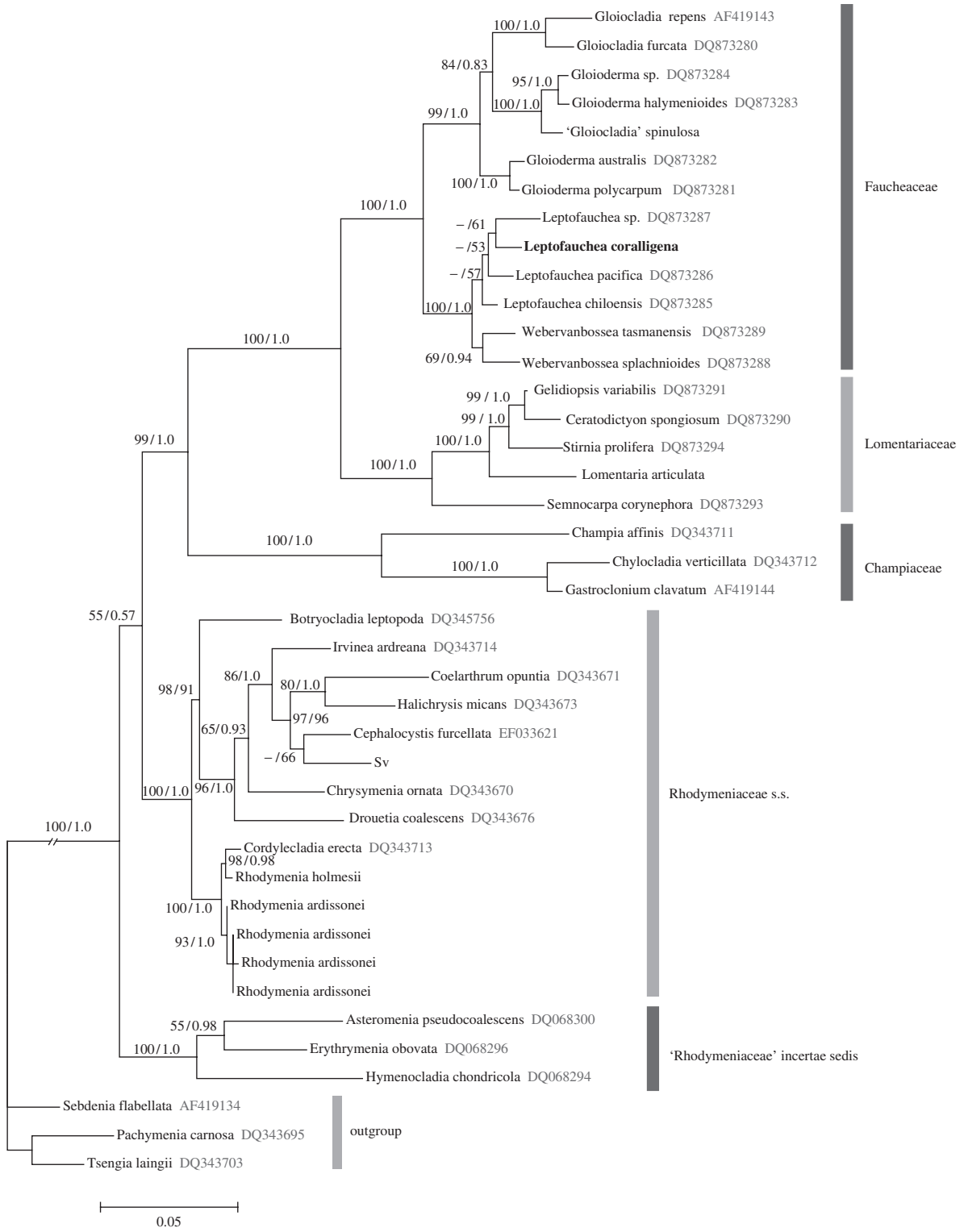


Fig. 44. Maximum likelihood phylogeny of the Rhodymeniales based on large subunit rDNA sequences, rooted with three representatives of related red algal orders. Node support values are given on each branch (ML bootstrap/BI posterior probabilities). The log-likelihood of the tree is −16541.47. Base frequencies are A: 0.252; C: 0.199; G: 0.297 and T: 0.250. The substitution rates are A–C: 0.719; A–G: 2.112; A–T: 1.636; C–G: 0.471; C–T: 3.731; G–T: 1. The proportion of invariable sites in the alignment is 0.570 and the shape parameter of the gamma distribution of among site rate heterogeneity is 0.560

become net-like. All cells of the *tela arachnoidea* are of medullary origin, as can be identified by the prominent inclusion of refractive bodies. Cells in the immediate vicinity of the procarp differentiate into the nutritive tissue.

In young cystocarps, the nutritive tissue is situated in the central part of the pericarp and subtended by cells of the *tela arachnoidea*. The nutritive tissue is displaced towards the bottom of the pericarp cavity by further gonimoblast

Figs 45–46. Habit of the holotypes *of Rhodymenia ardissonei* and *R. ligulata*. Fig. 45. *Rhodymenia ardissonei* (PAD 1937). Fig. 46. *Rhodymenia ligulata* (L 0650250). Scale bars: 1 cm

development. In mature cystocarps, it appears as though there is no *tela arachnoidea* between the basal nutritive tissue and the vegetative medullary cells. Therefore, it may appear that the *tela arachnoidea* is formed by the nutritive tissue, as noted by Sparling (1957), Sánchez & Rodríguez-Prieto (2005) and Rodríguez-Prieto *et al*. (2007).

The idea of the *tela arachnoidea* filling the entire pericarp including the space between the nutritive cells and the cystocarp bottom, was strikingly illustrated in *Gloioderma saccatum* (J. Agardh) Kylin by Sparling (1957). Identical cystocarpic development was illustrated for *Leptofauchea* by Dalen & Saunders (2007) and for *Gloiocladia repens* (C. Agardh) Sánchez & Rodríguez-Prieto (Rodríguez-Prieto *et al*., 2007). Interestingly, a procarp suspended in the central part of a cystocarp and surrounded by a network-like tissue also appears to be characteristic for the recently described genus *Grammephora* N'Yeurt & Payri (2007). The authors placed the genus in the Rhodymeniaceae. In our opinion, *Grammephora* would better be placed in the Faucheaceae on the basis of a *tela arachnoidea* and tetrasporangia which develop in nemathecia. It should be noted, however, that there is some discussion on the nature of tetrasporangia in *Leptofauchea*. Tetrasporangia were not reported by Kylin (1931) in the original description of *L. nitophylloides*, the generitype, but a recent account by Millar (1999) mentions oval sori with terminal, cruciately divided tetrasporangia. Dalen & Saunders (2007) pointed out that the ontogeny of tetrasporangia and of paraphyseal filaments of the type species requires further clarification, since, in all other species of the genus, tetrasporangia are grouped in well-defined nemathecia.

Leptofauchea coralligena is most similar to *R. ardissonei*. Female gametophytes are easily distinguished, since in *Leptofauchea* a clear *tela arachnoidea* develops in the pericarp cavity. Cystocarps of *R. ardissonei* are typical for the genus in that surrounding medullary cells do not stretch to form a network, but remain rounded or ovoid and the pericarp wall is clearly separated from the gonimoblast by an empty space (Ardissone, 1874; Rodríguez-Prieto, pers. obs.). Sterile specimens of *L. coralligena*, however, can be extremely difficult to tell apart from *R. ardissonei* because differences in vegetative morphology and anatomy are subtle. Literature reports of *R. ardissonei* are particularly hard to interpret because usually no distinction was made between specimens growing in shallow water habitats and those growing on deep water coralligenous concretions. We conclude that adult specimens of *R. ardissonei* are dark red in colour and somewhat cartilaginous. *L. coralligena* is slightly paler, occasionally whitish due to accumulation of floridean starch and always membranous. Also, medullary cells of *R. ardissonei* are more difficult to observe in surface view than those of *L. coralligena*. Disposition and size of cortical and medullary cells, however, do not unequivocally separate the species due to intraspecific variation through the different seasons. Interestingly, medullary cells of *L. coralligena* are characterized by conspicuous refractive bodies, which are absent in *R. ardissonei*. These can be easily observed in young specimens, both in surface view and transverse sections, but are less obvious or even impossible to observe in mature thalli with medullary cells containing large amounts of floridean starch. Refractive bodies are also difficult to observe in herbarium specimens. The presence of these structures has not been reported from any other *Leptofauchea* species so far.

Apart from being morphologically very similar, *L. coralligena* and *R. ardissonei* display very different ecological behaviour which was first reported

by Codomier *et al.* (1988). The authors distinguished between *R. ardissonei* from surface waters, forming imbricate mats on sponges and stipes of *Cystoseira* spp., and isolated specimens living on deep-water coralline concretions. These differences in growth form were, however, attributed to different substratum preferences and species boundaries within *R. ardissonei* were not questioned. According to Izquierdo (2003), the shallow specimens are perennial, and consequently, it is possible to find both young and adult specimens throughout the year, whereas the deep-water specimens form erect fronds on an annual basis.

It is also worth comparing *L. coralligena* with *Rhodymenia leptofaucheoides* P. Huvé & H. Huvé (1971), from deep water habitats in Tunisia. The name of the latter species is interesting in that it suggests morphological similarity to *Leptofauchea*. Indeed, *R. leptofaucheoides* is morphologically similar to *L. coralligena*, but the cortex is unilayered rather than composed of two layers of cells. The absence of female gametophytes prevented unambiguous placement of the species in either *Rhodymenia* or *Leptofauchea*. However, the presence of tetrasporangia confined to the apices (not to the subapical parts of the distal segments) and their disposition in sori rather than nemathecia, make placement in *Leptofauchea* unlikely.

Leptofauchea coralligena has been confirmed in the western Mediterranean Sea. Atlantic specimens attributed to *R. ardissonei*, recorded by Newton (1931, as *R. corallicola*) and also collected by the first author in Brittany, France (HGI-A 2131), appear to be structurally different and require further study.

Acknowledgments

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