Rhodymeniocolax mediterraneus sp. nov. (Rhodymeniales, Rhodophyta), parasitic on Rhodymenia ardissonei from the western Mediterranean Sea

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Rhodymeniocolax mediterraneus Vergés, Izquierdo & Verlaque sp. nov., a sublittoral adelphohemiparasite of Rhodymenia ardissonei from the western Mediterranean Sea, is described. The distinctive vegetative and reproductive characteristics of the new species are: plants generally less than 6 mm in height with terete to compressed axes up to 1(±2) mm broad; a cortex composed of one to three layers of cells; spermatangia arranged in sori located on the subapical part of the thallus; cystocarps laterally positioned on branches; and cruciate tetrasporangia borne in sori. A comparison is made with other parasitic genera of Rhodymeniales and other species of Rhodymeniocolax.

INTRODUCTION

As a part of the ‘Flora Phycologica Iberica’ project, which started with the monographs of Fucales (Gómez Garreta 2001) and Kallymenia J. Agardh (Vergés 2001), the monograph of Rhodymeniales is being carried out in the Iberian Peninsula at present (Izquierdo Ramírez 2003; Sánchez 2003). During the study of the genus Rhodymenia Greville (1830), a new species of parasitic Rhodymeniales was discovered on Rhodymenia ardissonei Feldmann. This species, previously reported from Corsica as Rhodymeniocolax sp. by Verlaque (1987), is described herein as Rhodymeniocolax mediterraneus Vergés, Izquierdo & Verlaque sp. nov.

MATERIAL AND METHODS

This study is based on Mediterranean specimens collected subtidally by scuba diving in Corsica (France) during May 1981 and July 1982, and intertidally in Catalonia (Spain) from September 2002 to May 2004. Specimens were collected from 0 to 7 m depth. Specimens were preserved in buffered 5% formaldehyde-seawater until further treatment. Transverse and longitudinal sections were made with a Criocut-1800 (Reichert-Jung) freezing cryotome, stained in acidified 1% aniline-blue distilled water, and mounted permanently in 50% Karo corn syrup. Drawings were made using a Labophot 2 Nikon microscope with a camera lucida and photographs using a Zeiss Axioskop 2 microscope with a digital camera.

Voucher specimens and slides were deposited in the Herbarium of the University of Girona, Spain (HGI), in the algae section with reference letters HGI-A, and the Herbarium of Marc Verlaque, Centre d’Océanologie de Marseille, France, with the reference letter: F (wet specimens).

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RESULTS

Rhodymeniocolax mediterraneus Vergés, Izquierdo & Verlaque sp. nov.

Figs 1–17

Diagnosis: Thallus 1–4(–6) mm altus, rami teretes vel compressi, 1–5 mm longi et 0.2–1(–2) mm lati, verrucosi si cystocarpia sunt; semiparasita in Rhodymenia ardissonei; structura multiaxialis, incrassatam corticem 1–3 cellulas latum et medullam pseudoparenchymato.
Reproduction. Gametangial thalli monoeccious, procarpic; spermangia in subapical sori, 1–3 µm in diameter; carpogonial branches four-celled and auxiliary branches two-celled borne on an inner supporting cell; carpogonial branches erect; basal fusion cell branched; ovoid to angular carposporangia, 4–10 µm in diameter, produced by each gonimoblast cell; basal nutritive tissue not conspicuous; erect filaments disintegrating around the gonimoblast; cystocarps protruding, often clustered, hemispherical, 200–675 µm across, ostiolate; tetrasporangia in subapical sori, 16–33 × 8–18 µm, decussately or cruciately divided.

Etymology: The epithet refers to the Mediterranean Sea, which is the type region.

Holotype: HGI-A 5836a, gametophyte with cystocarps, parasitic on Rhodymenia ardissonei, deposited at the University of Girona. Collected by C. Izquierdo on 18 May 2003, 0.5 m depth (eight microscope slides: S-5836a-1–S-5836a-8).

Isotypes: Isotype collection deposited at the University of Girona. Four sporophytes (HGI-A 5836b–e), two gametophytes (HGI-A 5836f–g) and eight microscope slides (S-5836b-1–S-5836b-8) realized with the specimen HGI-A 5836b.

Type locality: Cala St Francesc, Blanes (41°41′N, 2°48′E), Spain, Mediterranean Sea.

Selected specimens examined: Spain: Catalonia, BLANES – Cala St Francesc, 0.5 m depth, Cystoseira mediterranea Sauvageau community (C. Izquierdo: 19 May 2002, HGI-A 5845 †); 0.5 m depth, Corallina elongata J. Ellis & Solander community (C. Izquierdo: 16 June 2002, HGI-A 5809 †); 7 July 2002, HGI-A 5810 †; 1 September 2002, HGI-A 5846 †; 22 September 2002, HGI-A 5811 †; 30 March 2003, HGI-A 5814 †; Rhodymenia ardissonei community in a rocky hole (C. Izquierdo: 9 February 2003, HGI-A 5800 †; 18 May 2003, HGI-A 5836 †, HGI-A 5836b †, HGI-A 5836c †; 6 July 2003, HGI-A 5863 †). Calonge, Roques Planes, 0.5 m depth, Rhodymenia ardissonei community in a rocky hole (C. Izquierdo: 18 March 2003, HGI-A 5808 †; 14 May 2003, HGI-A 5834 †, HGI-A 5839 †); (N. Sánchez & A. Vergés: 30 May 2004, HGI-A 6313 †, 6314 †). Palamós, Punta del Moll, 0.5 m depth, Corallina elongata community (C. Izquierdo: 14 May 2003, HGI-A 5835 †). Palamós, Cala Fosca, 0.5 m depth, Rhodymenia ardissonei community in a rocky hole (C. Izquierdo: 25 April 2003, HGI-A 5825 †). Mataró, Platja del fortí, 0.5 m depth, Rhodymenia ardissonei community in a rocky hole (L. Polo & C. Izquierdo: 17 July 2003, HGI-A 5900 †).

France: Corsica. Galeria, 7 m depth, Halopteris filicina (Grateloup) Kützing & Rhodymenia ardissonei communities (M. Verlaque: 24 May 1981, F1229 †; 5 July 1982, F1269–F1271 †; 5 July 1982, F1272 †).

Distribution: Until now Corsica (France) and Catalonia (Spain), north-western Mediterranean, but distribution probably similar to that of the host Rhodymenia ardissonei, which is widely distributed in the Mediterranean Sea (Guiry & Nic Dhoonchaa 2005).

Fig. 5. Transverse section of the thallus (HGI-A 5808).
Fig. 6. Longitudinal section of the base showing small-celled filaments of the parasite between larger medullary cells of the host. Arrowheads: secondary pit-connections between the parasite and the host cells (HGI-A 5800). Scale bars = 500 µm (Figs 1, 2, 3), 3 mm (Fig. 4), 30 µm (Figs 5, 6).
Table 1. Comparison of *Rhodymeniocolax* and the other genera of parasites of the Rhodymeniales.1

| References | Champiocolax | Faucheocolax | Gloiocolax | Rhodymeniocolax |
|------------|--------------|--------------|------------|-----------------|
| Bula-Meyer (1985), Womersley (1996) | Setchell (1923), Sparling (1957), Hawkes & Scagel (1986) | Sparling (1957) | Setchell (1923), Sparling (1957), Irvine & Guiry (1983), Hawkes & Scagel (1986), Womersley (1996), this study |
| Number of species | 2 | 1 | 1 | 4 |
| Height (mm) | 1.0–4.0 | 1.0–4.5* | 1.0–1.5* | 0.75–6.0 |
| Thallus | hollow | solid | solid | solid |
| Diaphragms | present | absent | absent | absent |
| Cortical filaments | *Champa*-like | anticalinal | anticalinal | pseudoparenchymatous or anticalinal |
| Cortical layers | 1–2 | 7–8* | 7–8* | 1–3 (–6) |
| Gametophytes | in sori | m.d. | m.d. | monocious or dioecious |
| Spermangia | m.d. | m.d. | m.d. | in sori |
| Diameter (µm) | 2–4 | — | — | 1–4 |
| Sterile branch | absent | — | — | four-celled, slightly bent |
| Diameter (µm) | 250–1000* | 600* | m.d. | ostiolate |
| Cystocarps | persistent (telar achroinoida) | persistent (telar achroinoida) | persistent (telar achroinoida) | disintegrating |
| Vegetative erect filaments | present but very slight | present | m.d. | present |
| Diameter of carposporangia (µm) | 7–11 | 15–30* | m.d. | 4–12 |
| Tetrasporangia | tetrahedral, scattered over the thallus | cruciate, scattered over the thallus | cruciate, scattered over the thallus | decussate–cruciate, scattered over the thallus, in sori or nemathecia |
| Size (µm) | 29–42 × 14–25* | 15–26 × 10–13* | 13–33 × 8–13* | 16–33 × 8–18 |
| Hosts | *Champa* spp. | *Fauchea* spp. | *Gloiocladia* spp. | *Rhodymenia* spp. |
| Distribution | NW Atlantic (Caribbean), S Australia | NE Pacific (from British Columbia to California) | SW Pacific (New Zealand) | Mediterranean, NE Atlantic (British Isles), NE Pacific (from Washington to S California), S Australia |

1 *, From the illustrations by the authors; m.d., missing data.

**Habitat and Seasonality:** *Rhodymeniocolax mediterraneus* grows exclusively from 0 to 10 m depth on *Rhodymenia ardissoni*. The host is either directly attached to the rocky substratum or to sponges, as understory of large erect algae or as monospecific stand in rocky holes. The infected specimens of *R. ardissoni* are intermixed with uninfected ones. The parasite was never found below 10 m depth although R. ardissoni is frequent in the deep sublittoral assemblages. All the studied specimens were fertile. The gametophytes and tetrasporophytes sometimes occurred on the same host. The species was apparently absent on *R. ardissoni* collected in autumn (from October to December). A cryptic form (endoparasitic because pigmented) on *Rhodymenia* grows over the thallus, in sori or nemathecia. Cystocarps are formed in subapical sori on the branches. The outermost cortical cells elongate and form one or two spermatangial mother cells, up to 8 µm in diameter, that cut off outwardly one or two spermatangia measuring up to 3 µm in diameter. Spermatia are shed through mucilage that becomes very thick during spermatangial development (Fig. 7).

**Reproductive Structures:** The gametophytes are monocious. Spermatangia are formed in subapical sori on the branches. The cortical cells are 5–10 µm in diameter. The pseudoparenchymatous medulla, up to 1200 µm across, consists of nonpigmented, isodiametric to oblong cells, 100 µm long and 20–80 µm in diameter in the centre of the thallus and diminishing in diameter towards the cortex (Fig. 5). At the host–parasite interface, cells of the parasite creep between the cortical and medullary cells of the host without apparent modification to the host’s structure. Cells of both algae are contiguous and secondarily pit-connected (Fig. 6).

**Vegetative Structure:** The thallus structure is multiaxial. The cortex consists of one to three layers of rounded to ovoid cells. Outer cortical cells are 5–10 µm in diameter. The pseudoparenchymatous medulla, up to 1200 µm across, consists of nonpigmented, isodiametric to oblong cells, 100 µm long and 20–80 µm in diameter in the centre of the thallus and diminishing in diameter towards the cortex (Fig. 5). At the host–parasite interface, cells of the parasite creep between the cortical and medullary cells of the host without apparent modification to the host’s structure. Cells of both algae are contiguous and secondarily pit-connected (Fig. 6).

Plants are procarpic with four-celled carpogonial branches, which are slightly bent and positioned on a modified inner cell that acts as a supporting cell. The first three cells of the carpogonial branch are
angular in shape. The carpogonium is ovoid or round with a simple trichogyne (Fig. 8). The supporting cell, which is 17±28 μm in diameter, is round or occasionally ovoid and bears the two-celled auxiliary branch; 2nd, second cell of the carpogonial branch; 3rd, third cell of the carpogonial branch.

The transfer of the nucleus from the zygote to the auxiliary cell has not been observed after presumed fertilization. From the auxiliary cell, a primary gonimoblast cell is formed and acquires a ‘wineglass’ shape when the gonimoblast is young (Figs 9, 15). Later, the supporting cell, auxiliary mother cell, auxiliary cell and the primary gonimoblast cell form a large and elongated fusion cell (Figs 10, 11). The protein bodies in the auxiliary cell disappear and a deeply stained ring appears at the basal margin of the primary gonimoblast cell from which develop some thick gonimoblast filaments that form gonimolobes (Fig. 11). Most of the cells of the carposporophyte become carposporangia, which measure 4–8(–10) μm in diameter when young and 9–12(–18) μm when mature. The basal nutritive tissue is formed by ovoid cells (Figs 10, 13). Around the young gonimoblast there are some vegetative cells that become erect filaments, most of which disintegrate when the gonimoblast matures (Figs 10–12). The cystocarps are laterally inserted over the thallus and often clustered. The mature cystocarps, protruding, hemispherical, ostiolate, reach up to 625 μm in height (including the pericarp) and 200–675 μm in diameter. The pericarp, 80–125 μm thick, is formed by up to 13 layers of small round cells arranged in radial rows (Fig. 13).

The decussately or cruciately divided tetrasporangia, 16–33 × 8–18 μm, are basally pit-connected to the inner cortical cells and located in extensive sori near the apices of the thallus. The two to three outer cortical cells of tetrasporangial sori are elongated (Figs 16, 17).

**DISCUSSION**

The four adelphoparasitic (sensu Feldmann & Feldmann 1958) genera presently included in the Rhodymeniales, *Faucheocolax* Setchell (1923), *Rhodymeniocolax* Setchell (1923), *Gloiocolax* Sparling (1957) and *Champiocolax* Bula-Meyer (1985), are easily distinguishable by their host specificity and anatomical and reproductive features (Table 1). *Champiocolax* differs from the other genera by having a hollow thallus with monostromatic diaphragms, four-celled carpogonial branches, a *tela arachnoidea* (persistent distinctive network of cobweb-like filaments surrounding mature carposporophytes, Saunders et al. 1999) and tetrahedral tetrasporangia (Bula-Meyer 1985; Womersley 1996). *Faucheocolax* and *Gloiocolax* are characterised by anticlinal cortical filaments, three-celled carpogonial branches, the presence of a sterile branch on auxiliary mother cells and a *tela arachnoidea* (Sparling 1957; Hawkes & Scagel 1986). According to Sparling (1957, p. 345), the arrangement of the carpogonial branches in the parasitic genera of Rhodymeniales is not very valuable as a distinguishing feature, although in *Gloiocolax* the carpogonial branch is straight and in *Faucheocolax* is slightly bent. Lastly, *Rhodymeniocolax* is well characterised by being parasitic on *Rhodymenia* and in having a pseudoparenchymatous cortex (at least in the young part), four-celled carpogonial branches, no sterile branch on the auxiliary mother cells, disintegrating erect filaments between the gonimoblast and the pericarp and cruciate tetrasporangia.

Two species are currently assigned to the genus *Rhodymeniocolax*, *R. botryoidea* Setchell (1923, as *R. botryoidea*), the

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**Fig. 14.** Transverse section of female gametophyte showing an auxiliary cell branch prior to the development of the gonimoblast (HGI-A 5835).

**Fig. 15.** Vertical section of a carposporophyte showing primary gonimoblast cell extending gonimoblast filaments (HGI-A 5814). Scale bars = 10 μm (Figs 7–9), 50 μm (Fig. 10), 30 μm (Figs 11–13) and 20 μm (Figs 14, 15).

**Figs 16, 17.** Tetrasporangial features.

**Fig. 16.** Surface view of a tetrasporangial sorus with mature tetrasporangia (HGI-A 5800).

**Fig. 17.** Transverse section of a tetrasporangial sorus (HGI-A 5834). Scale bars = 20 μm (Figs 16, 17).
type species described from southern California and reported from northern Washington to southern California (Hawkes & Scagel 1986), and R. austrinus Womersley (1996) (as R. australis, see Silva 2004), described from southern Australia. A third species occurs in the British Isles and France but it is still unnamed (Irvine & Guiry 1983; Hiscock & Maggs 1984). The habit and anatomical and reproductive structures are very similar for all the species of Rhodymeniocolax; however, they grow on specific host(s) and there are some qualitative and quantitative differences (Table 2). The thallus is tuberculate with short and thick axes, the cystocarps are terminal and tetrasporangia are scattered over most of the thallus in R. botryoides. In R. austrinus anticalinal cortical filaments are found in old cortices, and tetrasporangia occur in extensive nemathecia. Although poorly known, the unnamed species from the Atlantic differs from the Mediterranean Rhodymeniocolax in having smaller dimensions (length and diameter of axes, medullary cells), a more extended cortex (up to five cortical layers) and cystocarps that are subterminal to terminal.

Lastly, R. mediterraneus differs from all the other species in the specific host (Rhodymenia ardissonii), in habit (simple or branched thallus up to 6 mm height, with terete to compressed branches up to 2.0 mm broad), and in having (1) a pseudoparenchymatous cortex, one to three cell layers thick; (2) cystocarps clustered and laterally inserted on branches; and (3) tetrasporangia in subapical sori.

Recent meticulous investigation showed that tetrasporangia are of intercalary origin in most of species of Rhodymeniaceae and reports of terminal tetrasporangia appear to be confined to particular species of the genus Rhodymenia but are seldom if ever substantiated by accurate development studies (cf. the review in Saunders et al. 1999). In Rhodymeniocolax mediterraneus, the material studied did not allow to solve the origin of tetrasporangia and only basal pit-connection of mature tetrasporangia to inner cortical cells was observed.

The genus Rhodymeniocolax is closely related to the anatomy and reproductive structures of its hosts, but differs in having: (1) a probably hemiparasitic way of life; (2) a highly reduced stature; (3) three layers of cortical cells; and (4) a medulla composed of more than two layers of ovoid to elongated cells that are not as large as their host's. There are limited data on the cystocarps of Rhodymenia ardissonii (Codomier et al. 1988) and the reproductive male and female structures are unknown, so comparisons cannot be made with those of Rhodymeniocolax mediterraneus (Table 3).

In conclusion, we propose that these criteria are sufficient to recognize R. mediterraneus as a new species. Saunders et al. (1999, p. 35) emended the definition of the four families

**Table 2. Comparison of the species of Rhodymeniocolax.**

| References | R. botryoides | R. austrinus | R. sp. | R. mediterraneus |
|------------|---------------|--------------|--------|-----------------|
| Distribution | NE Pacific (from Washington to S California) | S Australia | NE Atlantic (British Isles) | Mediterranean (Spain, France) |
| Hosts | Rhodymenia pacifica Kylin | Rhodymenia sonderi P.C. Silva (= R. australis Sonder) | Rhodymenia spp. | Rhodymenia ardissonii Feldmann |
| Thallus | tuberculate to short compact filaments | simple or few branched | simple or branched | simple or few branched |
| Size (mm) | 2–4 (diameter) 1–3 (±4) (height) | 1–5 (height) | 5 (diameter) | 14–6 (height) |
| Axes | short and thick | terete to compressed | terete to slightly compressed | terete to compressed |
| Length (mm) | 0.75 | 1.0–1.5 (±2.0) | 2.0 | 1.0–5.0 |
| Diameter/width (mm) | 0.8–1.0* | 0.3–0.6 (±1.5) | 0.75 | 0.2–1.0 (±2.0) |
| Cortex | pseudoparenchymatous to short compact filaments | pseudoparenchymatous to anticlinal filaments | m.d. pseudoparenchymatous |
| Cortical layers | 1–4* | 2–6 | 1–5 | 1–3 |
| Larger medullary cells, diameter (μm) | m.d. | 50–120 | 15–50 | 20–60 (±80) |
| Monococious/dioecious | m.d. | dioecious | m.d. | monococious |
| Carpogonial branches | four-celled | four-celled | m.d. | four-celled |
| Location of cystocarps on the axes | terminal | lateral | subterminal to terminal | lateral |
| Diameter of cystocarps (μm) | 500–600* | 400–600 immature | 200–675 | 4–10 |
| Ostiulate | yes* | yes m.d. | yes disintegrating | m.d. |
| Vegetative erect filaments | m.d. | disintegrating | m.d. | disintegrating |
| Diameter of carposporangia (μm) | 6–12 | 2–4 | 2–4 | 1–3 |
| Arrangement of spermangia | in sori | scattered over most of the thallus, cortex unmodified | unknown in sori | in sori, cortex slightly modified |
| Arrangement of tetrasporangia | in extensive nemathecia | unknown | m.d. | unknown |
| Size (μm) | 17–22 × 9–12* | 20–30 × 8–14 | — | 16–33 × 8–18 |

1 * From the illustrations by the authors; m.d., missing data.
of the order Rhodymeniales based on a molecular-systematic investigation. The new species described in this paper fulfills almost all the characters of the emended family of the Rhodymniaceae.

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Table 3. Comparison of Rhodymenicolax mediterraneus and its host Rhodymenia ardissoeni.

| Character                  | Rhodymenia ardissoeni | Rhodymenicolax mediterraneus |
|----------------------------|-----------------------|------------------------------|
| References                 | Codomier et al. (1988), Izquierdo Ramírez (2003) | this study                   |
| Way of life                | autotrophic           | hemiparasitic                |
| Height (mm)                | <50–60                | 1–4 (–6)                     |
| Cortical layers            | 1–2                   | 1–3                          |
| Medullary layers           | 2                     | >2                           |
| Larger medullary cells (μm)| 80–150 × 40–60        | 100 × 80                     |
| Carpogonial branches       | unknown               | four-celled                  |
| Vegetative erect filaments | absent                | disintegrating               |
| Diameter of cystocarps (μm)| 600–700              | 200–675                      |
| Ostiole                    | present               | present                      |
| Spermatangia               | unknown               | in sori                      |
| Tetrasporangia             | cruciate, in sori     | decussate-cruciate, in sori  |
| Size (μm)                  | 25–28 × 15–18         | 16–33 × 8–18                 |

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