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Rugulopteryx (Dictyotales, Phaeophyceae), a genus recently introduced to the Mediterranean

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The introduction of a common Western Pacific representative of the Dictyotales, *Rugulopteryx okamurae* (Dawson) I.K. Hwang *et al.*, in european waters was demonstrated for the first time. The species was collected in the coastal lagoon of Thau (France, Mediterranean) in 2002. The specimens from Europe are described and compared with *R. okamurae*. Their conspecificity with northwest Pacific populations is confirmed based on morphological and comparative sequence analysis of the plastid-encoded *psb*A gene. *Rugulopteryx okamurae* is probably introduced in the Thau lagoon along with Japanese oysters, *Crassostrea gigas* (Thunberg 1793), imported into Europe for mariculture purposes. Since its introduction, although reproductive structures were not observed, *R. okamurae* has established self-sustaining populations without displaying an invasive behaviour. *Rugulopteryx okamurae* can be expected to turn up wherever *C. gigas* is reared.

KEY WORDS: *Rugulopteryx okamurae*, Marine algae, Species introduction, France, Mediterranean

INTRODUCTION

In spring 2002, a population of a species of Dictyotales hitherto unknown in the Mediterranean Sea was discovered close to a small harbour of the Thau Lagoon (France) by the first author. The individuals, which lacked reproductive structures, were characterized by a dichotomously branched thallus with a medulla one cell thick centrally and two to three cells thick near the margins. This anatomical feature is only known in few species belonging to three genera of the tribe Dictyoteae J. Agardh (1882, 1894): *Dictyota intermedia* Zanardini, *D. pinnatifida* Kützing, *Dilophus*[1] *crinitus* J. Agardh, *D. fastigiatus* (Sonder) J. Agardh, *D. gunnianus* J. Agardh, *D. robustus* (J. Agardh) Womersley, *Rugulopteryx marginata* (J. Agardh) De Clerck & Coppejans, *R. okamurae* (Dawson) I.K. Hwang, W.J. Lee & H.S. Kim, *R. radicans* (Harvey) De Clerck & Coppejans and *R. suhrii* (Kützing) De Clerck & Coppejans (Womersley 1987; De Clerck 2003; De Clerck *et al.* 2006; Hwang *et al.* 2009). All these species are restricted to the Pacific and the southern reaches of the Indian Ocean, except for *Dictyota pinnatifida*, a taxon described from Antigua, Lesser Antilles (Kützing 1859), and widely reported in the central Atlantic Ocean (from Bermuda to Brazil and from Madeira to Cape Verde Islands) (John *et al.* 2004; Guiry & Guiry 2008). Since *D. pinnatifida* has a distinctive alternate branching pattern that differs from the dichotomous branching pattern of our specimens, we considered the possibility of a species introduction from the Pacific or Indo-Pacific ocean.

The Thau Lagoon is known as a hot spot of marine species introductions in Europe with Japan and Korea as major donor regions (Verlaque 2001). Consequently, on the basis of morphological data and a likely Asiatic origin, we provisionally attributed our material to *R. okamurae* (Verlaque *et al.* 2007, as *Dictyota okamurae*), a species described from Japan and widely distributed in northwest Asia. In the present study we give a description of the Mediterranean specimens, and we confirm their identity by molecular analyses.

MATERIAL AND METHODS

Specimen collection and herbariums

Observations and sampling in the Thau Lagoon were performed from April 2002 to July 2008. Samples were hand collected and preserved in buffered 4% formaldehyde–seawater or in silica gel prior to DNA isolation. Fixed material was studied under the light microscope. Material was sectioned manually with a razor blade. Transverse sections were stained with 1% aqueous Aniline Blue, washed, and then acidified by the addition of a drop of 1 N HCl. Photomicrographs were made using a Nikon Optiphot-2®.

MATERIAL STUDIED: Thau Lagoon, France (see Fig. 1 for details of locations): H7645, Le Mourre Blanc, April 2002,

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[1] The genus *Dilophus* was provisionally retained by De Clerck *et al.* (2006) because the generitype, *Dilophus gunnianus*, was not included in their molecular analyses. Consequently, only those species that had been shown to belong to an emended genus *Dictyota* were formally transferred. A limited number of species awaits study prior to potential taxonomic changes.

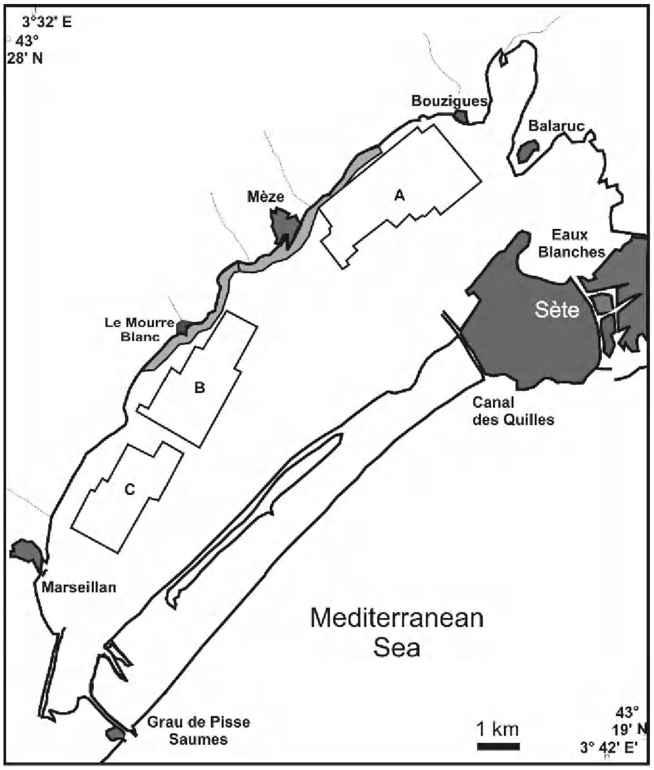


Fig. 1. The Thau Lagoon, with locations of oyster farming zones (A, B, C) and *Rugulopteryx okamurae* populations (in grey) (spring 2008).

0.5-m depth; H7650–7651 and H7654–7655, Mèze, September 2002, 1–2-m depth; H7643 & 7653, Mèze, June 2005, 1–2-m depth; H7652, Le Mourre Blanc, June 2005, 0.5-m depth; FS280 & 281, Mèze, July 2008, 0.5-m depth.

The above material has been deposited in the Herbarium Verlaque, COM, Marseille, France. Specimens used in the molecular analyses (Table 1) were deposited in the Biology Department of Ghent University.

Phylogenetic analyses

Total genomic DNA was extracted using a standard CTAB-extraction method and subsequent purification with a Wizard® DNA Clean-Up System (Promega Inc., Madison, WI, USA) as outlined in De Clerck *et al.* (2006). The plastid-encoded *psb*A gene (photosystem II reaction center protein D1) was amplified and sequenced using primers listed by Yoon *et al.* (2002). Thirteen newly generated sequences (see Table 1) were complemented with a selection of sequences previously published by De Clerck *et al.* (2006) and Hwang *et al.* (2009). Taxon sampling aimed to represent the diversity of Dictyoteae species in the western Mediterranean Sea. Sequences were aligned by eye using BioEdit 7.0.4.1 (Hall 1999) and analysed under maximum parsimony (MP) as well as using a likelihood approach. Maximum likelihood (ML) analyses were carried out with PhyML (Guindon & Gascuel 2003). MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001) was used for Bayesian phylogenetic inference (BI). A GTR+I+G model was used to analyse the data set under ML with parameters estimated by PhyML: base frequencies ($A = 0.25$, $C = 0.18$, $G = 0.20$, $T = 0.36$), substitution matrix ($A\text{-}C = 0.300$, $A\text{-}G = 2.424$, $A\text{-}T = 2.274$, $C\text{-}G = 0.000$, $C\text{-}T = 6.280$, $G\text{-}T = 1.0$), gamma distribution shape parameter $\alpha = 0.329$, proportion of invariable site = 0.439.

RESULTS

Rugulopteryx okamurae (Dawson) I.K. Hwang, W.J. Lee & H.S. Kim

Figs 2–9

BASIONYM: *Dilophus okamurae* E.Y. Dawson (1950, p. 86).

SYNONYMS: *Dictyota marginata* Okamura (1913), *nom. illeg.*, *Dilophus marginatus* (Okamura) Okamura (1915), *nom. illeg.*, *Dictyota okamurae* (E.Y. Dawson) I. Hörnig, R. Schnetter & W.F. Prud'homme van Reine (1992, 1993). We refer to Hwang *et al.* (2009) for a detailed account on the complicated nomenclature of the species.

SYNTYPE LOCALITIES: Japan, Hizen (Kyūshū), Iyo (Shikoku), Sagami, Iwaki and Rikuzen (E. Honshū) Provinces.

Description of Thau Lagoon specimens

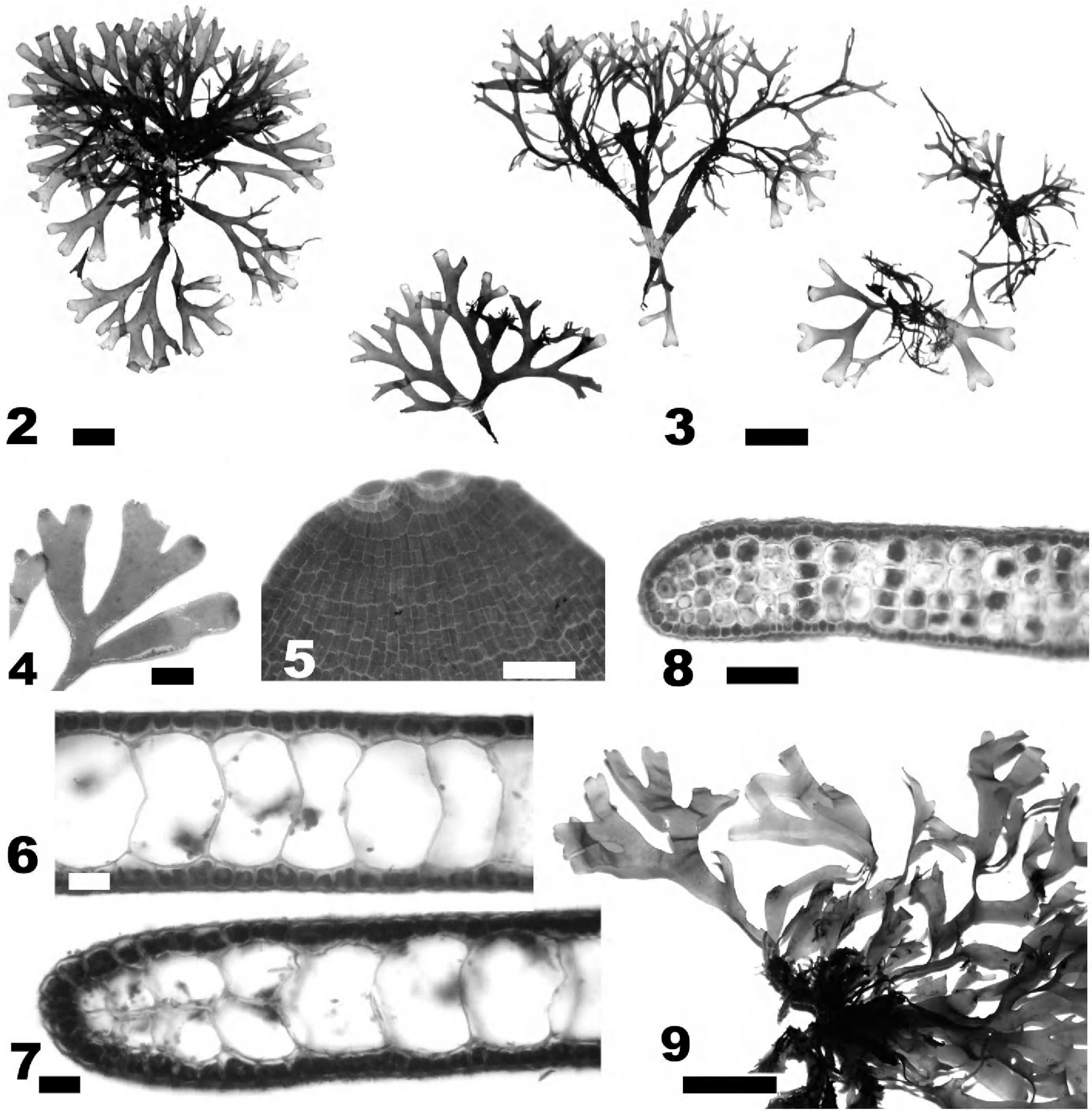
Thalli are membranous, erect, in bushy tangled clumps, up to 10 cm in diameter, attached to the substrate by means of multicellular, uniseriate, hyaline rhizoids and stolon-like segments, which grow up into new fronds; fronds are dichotomously branched in flabellate manner, up to 5 cm high; adventitious branchlets occur on the blade margins as well as at damaged portions (Figs 2, 3); colour *in situ* is yellow brown to darker when old, not iridescent; apices are obtuse to slightly emarginated (Figs 4, 5); segments, 3.0–11.3 mm long, expand in cuneate form beneath dichotomies, 2.5–6.0 mm broad; the margin is entire and thickened as if provided with a hem; in upper and mid parts of thallus, the medulla is one cell thick centrally, and two to three cells thick near the margins (Figs 6, 7); in lower parts of thallus, the medulla is composed of three to four layers of polygonal, thick-walled cells, 20–60 × 20–60 µm in transverse section (Fig. 8). Reproductive structures have not been observed.

Phylogenetic analyses

The data set consisted of 850 characters of 31 *psb*A sequences belonging to 20 different species. *Scoresbyella profunda* Womersley and *Dilophus fastigiatus* (Sonder) J. Agardh were used as out-group taxa. Only the consensus tree resulting from the Bayesian analysis is shown in Fig. 10. The ML tree ($\ln L = -3416.979$) was largely congruent with BI trees. The maximum parsimony analysis (using a Goloboff weighting with $K = 2$) resulted in a single most parsimonious tree that differed substantially from the trees generated using a likelihood approach. All analyses, however, are congruent in resolving the respective genera of the Dictyoteae (*Canistrocarpus*, *Rugulopteryx* and *Dictyota*) with high support. Low support values, bootstrap percentages as well as posterior probabilities are most likely to be

Table 1. List of species, collection sites, voucher specimens, collection dates (or) references, with GenBank accession numbers. New accession numbers associated with this study are given in bold.

Taxa	Collecting data/reference	GenBank accession number
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	Philippines: Olango Island, H. Verbruggen, 25.i.2004, HV631 (Hwang *et al.* 2009)	EU395603
C. crispatus (J.V. Lamouroux) De Paula & De Clerck	Philippines: Eastern samar, Guiuan, D.A. Payo, 5.viii.2003, DAP048 (Hwang *et al.* 2009)	EU395605
Dictyota acutiloba J. Agardh	Hawaii: O. De Clerck, 25.iv.2003, ODC888 (Hwang *et al.* 2009)	EU395602
D. ceylanica Kützing	French Polynesia: Tahiti, H. Verbruggen, 21.v.2002, HV214a (Hwang *et al.* 2009)	EU395607
D. ciliolata Sonder ex Kützing	Philippines: Olango Island, H. Verbruggen, 25.i.2004, HV632 (Hwang *et al.* 2009)	EU395604
D. coriacea (Holmes) I.K. Hwang *et al.*	California: Orange County, S. Murray, 23.xi.2004, CSUF003 (Hwang *et al.* 2009)	EU395619
D. dichotoma (Hudson) J.V. Lamouroux	France: Nord – Pas de Calais, Audresselles, O. De Clerck, 16.x.2004, ODC1027	EU395606
D. dichotoma	France: Brittany: Pointe de Mousterlin (F. Steen & J. Hollants, 06.vii.2008, FS160)	**FJ869842**
D. dichotoma	France: Brittany: Pointe de Mousterlin (F. Steen & J. Hollants, 06.vii.2008, FS161)	**FJ869843**
D. dichotoma	France: Provence: Sausset-les-Pins (F. Steen, J. Hollants & M. Verlaque, 08.vii.2008, FS247)	**FJ869840**
D. dichotoma	France: Provence: Sausset-les-Pins (F. Steen, J. Hollants & M. Verlaque, 08.vii.2008, FS252)	**FJ869841**
D. fasciola (Roth) J.V. Lamouroux	France: Languedoc-Roussillon: Banyuls: Cap du Troc (O. De Clerck, 24.v.2005, ODC1052)	**FJ869848**
D. fasciola	France: Languedoc-Roussillon: Banyuls: Cap du Troc (O. De Clerck, 24.v.2005, ODC1054)	**FJ869849**
D. fasciola	France: Languedoc-Roussillon: Banyuls: Cap du Troc (O. De Clerck, 24.v.2005, ODC1057)	**FJ869846**
D. fasciola	France: Languedoc-Roussillon: Cerbère: Cap Peyrefite (O. De Clerck, 26.v.2005, ODC1066)	**FJ869847**
D. intermedia Zanardini	Australia: Queensland, Keppel Bay, Yeppoon, T. Cowling, 18.viii.2005, TC1 (Hwang *et al.* 2009)	EU395615
D. jamaicensis W.R. Taylor	Jamaica: St. Ann Parish, H. Verbruggen, 15.viii.2004, HV926 (Hwang *et al.* 2009)	EU395608
D. kunthii (C. Agardh) Greville	Chile: Pan de Azucar, S. Faugeron, viii. 2004, Chile-M1 (Hwang *et al.* 2009)	EU395618
D. naevosa (Suhr) Montagne	Kwazulu-Natal: Mission Rocks, O. De Clerck & F. Leliaert, 13.vi.2003, KZN2241 (Hwang *et al.* 2009)	EU395609
D. pinnatifida Kützing	Jamaica: St. Ann Parish, H. Verbruggen, 12.viii.2004, HV902 (Hwang *et al.* 2009)	EU395612
D. sandvicensis Sonder	Hawaii: Oahu, O. De Clerck, 25.iv.2003, ODC896 (Hwang *et al.* 2009)	EU395611
D. spiralis Montagne	France: Provence: Sausset-les-Pins (F. Steen, J. Hollants & M. Verlaque, 08.vii.2008, FS230)	**FJ869839**
D. spiralis	France: Provence: Cassis: Cap Canaille (F. Steen, J. Hollants & M. Verlaque, 08.vii.2008, FS301)	**FJ869838**
D. spiralis	France: Provence: Cassis: Cap Canaille (F. Steen, J. Hollants & M. Verlaque, 08.vii.2008, FS302)	**FJ869837**
Dilophus fastigiatus (Sonder) J. Agardh	South Australia: Esperance Bay, N. Goldberg, 3.iv.2003, D96 (Hwang *et al.* 2009)	EU395614
Rugulopteryx okamurae (Dawson) I.K. Hwang *et al.*	South Korea: Haegeumgang, I.K. Hwang, 11.vii.1996, D194 (Hwang *et al.* 2009)	AY748322
R. okamurae	France: Languedoc-Roussillon: Lagune de Thau: Mèze (F. Steen, J. Hollants & M. Verlaque, 09.vii.2008, FS280)	**FJ869844**
R. okamurae	France: Languedoc-Roussillon: Lagune de Thau: Mèze (F. Steen, J. Hollants & M. Verlaque, 09.vii.2008, FS281)	**FJ869845**
R. radicans (Harvey) De Clerck & Coppejans	South Australia: Esperance Bay, N. Goldberg, 2.xi.2002 (Hwang *et al.* 2009)	EU395610
R. suhrii (Kützing) De Clerck & Coppejans	Kwazulu-Natal: Palm Beach, O. De Clerck *et al.*, 11.xi.2003, KZN-b 2346 (Hwang *et al.* 2009)	EU395617
Scoresbyella profunda Womersley	Western Australia: Geographe Bay, J.M. Huisman, x. 2003 (Hwang *et al.* 2009)	EU395620



Figs 2–9. *Rugulopteryx okamurae* (Dawson) I.K. Hwang, W.J. Lee & H.S. Kim from the Thau Lagoon.
Figs 2–3. Habit (H7643 and H7652, June 2005). Bars = 1 cm.
Fig. 4. Upper portion of thallus (H7643). Bar = 5 mm.
Fig. 5. Detail of an apical portion of thallus with two apical cells (H7643). Bar = 100 μm
Fig. 6. Transverse section of thallus, detail of the middle part with one layer of medullary cells (H7643). Bar = 20 μm.
Fig. 7. Transverse section of thallus, detail of the margin with two layers of medullary cells (H7643). Bar = 20 μm.
Fig. 8. Transverse section of thallus, detail of the basal portion with several layers of medullary cells (H7643). Bar = 100 μm.
Fig. 9. Habit of a wet specimen with undulate straps (H7643). Bar = 1 cm.

the result of insufficient signal in the *psb*A sequences to assess interspecific relationships with confidence. The gene, however, does contain enough information to assign intraspecific sequences to the same species as is reflected in the high support for the individual species represented by more than one specimen: *Dictyota dichotoma*, *D. fasciola*, *D. spiralis* and *Rugulopteryx okamurae*. Samples of *R. okamurae* collected in the Thau Lagoon invariably clustered

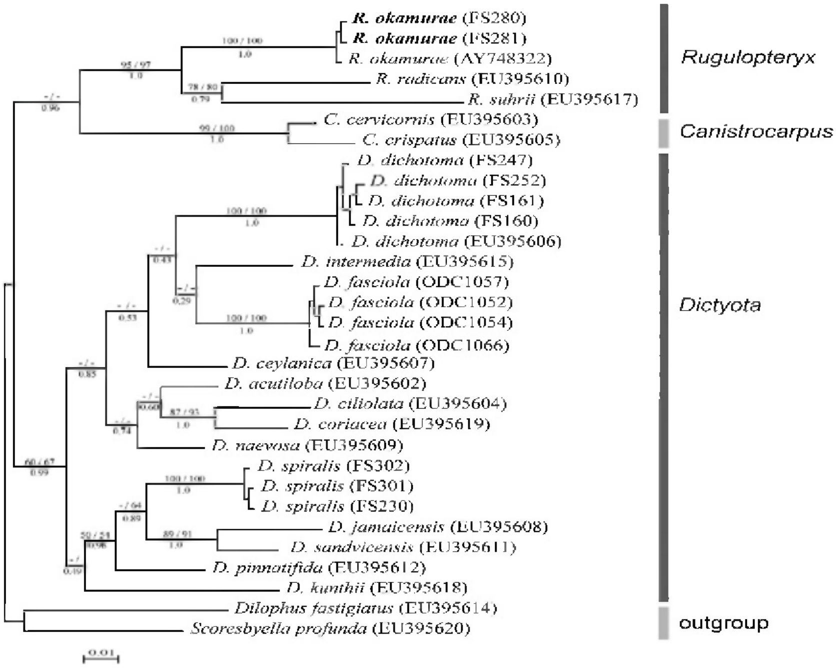


Fig. 10. Majority rule consensus tree resulting from the Bayesian analysis of the *psb*A data set, rooted with *Scoresbyella profunda* and *Dilophus fastigiatus*. Node support values are given at each ramification of the tree: bootstrap percentages (MP/ML) above edges, posterior probabilities below the edges. Branch lengths are proportional to the number of substitutions per site (see scale bar). GenBank accession numbers are provided for previously published sequences; newly generated sequences are identified by their collector numbers.

with a Japanese isolate of that species. Sequences of French and Japanese samples showed minimal sequences divergence (uncorrected p-distance: <0.1%).

Distribution and seasonality

Since the discovery of a small population near Mèze in spring 2002, *Rugulopteryx okamurae* has become established in 2008 along the north coast of the Thau Lagoon, from the north of Mèze to "Le Mourre Blanc" (Fig. 1). *Rugulopteryx okamurae* is abundant from spring to autumn (April–September). We have no observations for winter. It grows between the water surface and 2-m depth on rocky substrata. Fertile individuals were not observed so far.

DISCUSSION

Identity of the introduced *Rugulopteryx* of the Thau Lagoon

In the tribe Dictyoteae J. Agardh, species having a medulla one cell thick centrally and two to three cells thick near the margins have been described in the genera *Dictyota* J.V. Lamouroux (1809), *Dilophus* J. Agardh (1882) and *Rugulopteryx* De Clerck & Coppejans in De Clerck *et al.* (2006). Mediterranean specimens from the Thau Lagoon agree with the descriptions of *R. okamurae* of the northwest Pacific Ocean (Okamura 1913; Tseng 1984; Noda 1987; Hwang *et al.* 2009), and no differences in the molecular marker considered here were observed between our specimens and Korean populations (Hwang *et al.* 2009). Consequently, in spite of the absence of reproductive structures, the species discovered at Thau is attributed to *R. okamurae*. The species and the genus are new to European shores, all *Rugulopteryx* species being confined to the temperate waters of the northwest Pacific Ocean (*R. okamurae*), Australia (*R. marginata* and *R. radicans*) and South Africa (*R. suhrii*) (De Clerck *et al.* 2006; Guiry & Guiry 2008; Hwang *et al.* 2009). Contrary to the thallus of Korean populations that are flat (Hwang *et al.* 2009), Mediterranean specimens show an undulate thallus (Fig. 9) that agrees with pictures of *R. okamurae* from Japan (Sotogawa-cho, Choshi, Chiba Prefecture) of Haga (2008). The undulate nature of the fronds was originally defined by De Clerck *et al.* (2006) as a diagnostic character of the genus, but doubt arose on the taxonomic value of the character when Korean specimens of *R. okamurae* were reported to possess flat, nonundulate fronds.

The discovery of *Rugulopteryx okamurae* into the Thau Lagoon is the first case of introduction of a representative of the tribe Dictyoteae demonstrated hitherto in Europe. Our present knowledge of the *Dictyota* and related genera does not allow the interpretation of the observed European diversity in the light of recent anthropogenic introductions versus the presence of native but cryptic species. It may come as no surprise that *R. okamurae* is one of the few species that is well characterized morphologically and hence relatively easy to identify (Hwang *et al.* 2009). The analysis of the native or exotic origin of the other European species requires a more extensive sampling.

Vector, date and origin of the introductions

The 70-km^2 Thau Lagoon (southern France) is by far the leading site of oyster culture in the Mediterranean Sea, with a standing stock of 25,000 tons and an annual production of 12,000–13,000 tons of Japanese oysters, *Crassostrea gigas* (Thunberg) (Hamon & Tournier 1990; Trousselier *et al.* 1991). From 1971 to 1977, to restore a livestock decimated by parasites and pathogens, massive amounts of *C. gigas* were imported from the North Pacific (Japan, British Columbia) (Grizel & Héral 1991). As a result of the failure in the decontamination processes and/or quarantine of these imports, a first contingent of Pacific macrophytes from Japan was introduced (Verlaque 2001; Verlaque *et al.* 2007). Since 1977, the only spat officially imported to the Thau Lagoon was produced on European shores of the Atlantic. However, approximately 30 years after the massive importations from Japan, new exotic species are still being discovered (Verlaque *et al.* 2005, 2007). *Rugulopteryx okamurae* belongs to this new contingent of introduced species. This find confirms that importations of oysters from the northwest Pacific (most likely from Japan in the present case) have occurred in Europe after 1977, such as in 1994 when Korean oyster imports were discovered in Europe (see Verlaque 1996).

Probability of spread and risks of invasion

Rugulopteryx okamurae is widely distributed in Japan, with the exception of the coldest regions (north and east of Hokkaido) (Yoshida *et al.* 1990; Tokuda *et al.* 1994; Yoshida 1998). In the Pacific Ocean, the species was also recorded from China (Fujian Province) (Tseng 1984, as *Dilophus okamurae*), Korea (Lee & Kang 1986, as *Dictyota okamurae*; Chung 2007, as *Dilophus okamurae*; Lee 2008, as *Dictyota okamurae*), Philippines (Silva *et al.* 1987, as *Dilophus okamurae*) and Taiwan (Huang 2000, as *Dilophus okamurae*). Records from Mexico (Dawson 1950, as *Dilophus okamurai*) require additional confirmation. The species usually grows on the lower intertidal rocks (Tseng 1984), near the low-tide mark, and to a depth of several metres (Tokuda *et al.* 1994); although, it was reported to 35-m depth (Kajimura 1992). In Korea, *R. okamurae* is abundant year-round with a maximum growth and development of reproductive structures when seawater temperatures exceed 15°C. In the field, no gametophytes were observed, and sporophytes apparently exclusively recycle the diploid life history stage. Moreover, *R. okamurae* readily forms propagules (proliferous branchlets arising on the thallus surface), which grow into new plants (Kajimura 1992; Hwang *et al.* 2009). Such a vegetative propagation might explain the naturalization of the species in the Thau Lagoon despite the apparent lack of reproduction. Moreover, the species contains feeding-inhibitory substances that can reduce the intensity of predation (Tokuda *et al.* 1994). As far as the risk of invasion is concerned, *R. okamurae* does not display an invasive behaviour at Thau. Seven years after its discovery, its populations are restricted to the north coast of the lagoon, and the species has never been found in the open sea. However, *R. okamurae* is a common species widely distributed in the subtropical to temperate western Pacific; therefore, the climatic conditions of the Mediterranean and southern part of the North Atlantic coasts seem favourable to its survival. Moreover, since transfers of shellfish livestock occur regularly between the Thau Lagoon and the other European Mediterranean and Atlantic aquaculture sites (Mineur *et al.* 2007; Verlaque *et al.* 2007), the risk of secondary dispersal of *R. okamurae* in Europe appears high.

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