

Codium pulvinatum (Bryopsidales, Chlorophyta), a new species from the Arabian Sea, recently introduced into the Mediterranean Sea

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ABSTRACT: *Codium pulvinatum* sp. nov. (Bryopsidales, Chlorophyta) is described from the southern shores of Oman and from the Mediterranean shore of Israel. The new species has a pulvinate to mamillate–globose habit and long narrow utricles. Molecular data from the *rbcL* gene show that the species is distinct from closely related species, and concatenated *rbcL* and *rps3–rpl16* sequence data show that it is not closely related to other species with similar external morphologies. The recent discovery of well-established populations of *C. pulvinatum* along the central Mediterranean coast of Israel suggests that it is a new Lessepsian migrant into the Mediterranean Sea. The ecology and invasion success of the genus *Codium*, now with four alien species reported for the Levantine Sea, and some ecological aspects are also discussed in light of the discovery of the new species.

KEY WORDS: *Codium pulvinatum*, Israel, Lessepsian migrant, Levantine Sea, Oman, *rbcL*, *rps3–rpl16*

INTRODUCTION

Seaweed surveys in Oman at the beginning of the 21st century documented a distinctive *Codium* with a globose to pulvinate habit, which was initially identified as *Codium ovale* Zanardini by Schils & Coppejans (2003) and as *Codium minus* (O.C.Schmidt) P.C.Silva by Wynne (2004). The Omani material was later referred to as ‘*Codium* cf. *minus*’ by Verbruggen *et al.* (2007, 2012) but recognized to be genetically distinct from the Japanese species *C. minus* and to be distinct from material of *C. ovale* from Fiji or *Codium recurvatum* Verbruggen from Tanzania. Sequences of the genuine *C. minus* from Japan were initially published by Shimada *et al.* (2004). According to Verbruggen *et al.* (2007, 2012), the Omani *Codium* represents an example of convergent evolution with *C. minus* and deserves recognition at the species level. More recently, this same undescribed species was found on the Israeli coast of the Levantine Sea. The purpose of this paper is to formally describe this taxon as *Codium pulvinatum*, to investigate its relationships with other *Codium* species and to provide an account of its introduction into the eastern Mediterranean Sea.

MATERIAL AND METHODS

Voucher specimens that have been used in this study are housed in the following herbaria: BM, GENT, MICH, ON and ‘TAU’ (the Herbarium of Tel Aviv University). Herbarium abbreviations follow Thiers B (continuously

updated), except for ‘TAU’. All investigated specimens are listed in Table S1 (collecting data table).

Specimens examined were collected during seaweed surveys from the drift and subtidal of the Arabian Sea shores of southern Oman and the Levantine shores of Israel (Fig. 1). Ecological data such as environmental factors and habitat details were recorded while sampling. Specimens of the Omani material were pressed in the field and preserved in dilute (4%) formalin-seawater. The wet-preserved material in MICH was examined under a compound microscope (Carl Zeiss, Jena, Germany), and images of utricles and gametangia were made with a *camera lucida* attached to the microscope. Pressed and alcohol-preserved specimens of the Mediterranean collections were also prepared and deposited in ‘TAU’. Specimens were examined with a Zeiss Axioplan 2 imaging compound microscope (Carl Zeiss) and Olympus MVX10 Research Macro Zoom Microscope (Olympus Corp., Tokyo, Japan). Images were acquired with an Olympus DP71 microscope digital camera and an Olympus SP820UZ digital camera (Olympus Corp.). Morphological characteristics of the specimens were compared to the features of currently recognized taxa of *Codium* that have the same external pulvinate to mamillate–globose habit.

DNA extraction used the Wizard Genomic DNA Purification kit (Promega, Sydney, Australia) and amplification of the *rbcL* gene followed Verbruggen & Costa (2015). Sanger sequencing was outsourced to Macrogen (Seoul, Korea). Two separate datasets were generated, the first containing only a single specimen per species and both the *rbcL* and *rps3–rpl16* loci concatenated. This dataset served to infer the phylogenetic position of the target species. The second dataset contained multiple *rbcL* sequences of the target species and its closest relatives and served to explore haplotype diversity within and between species.

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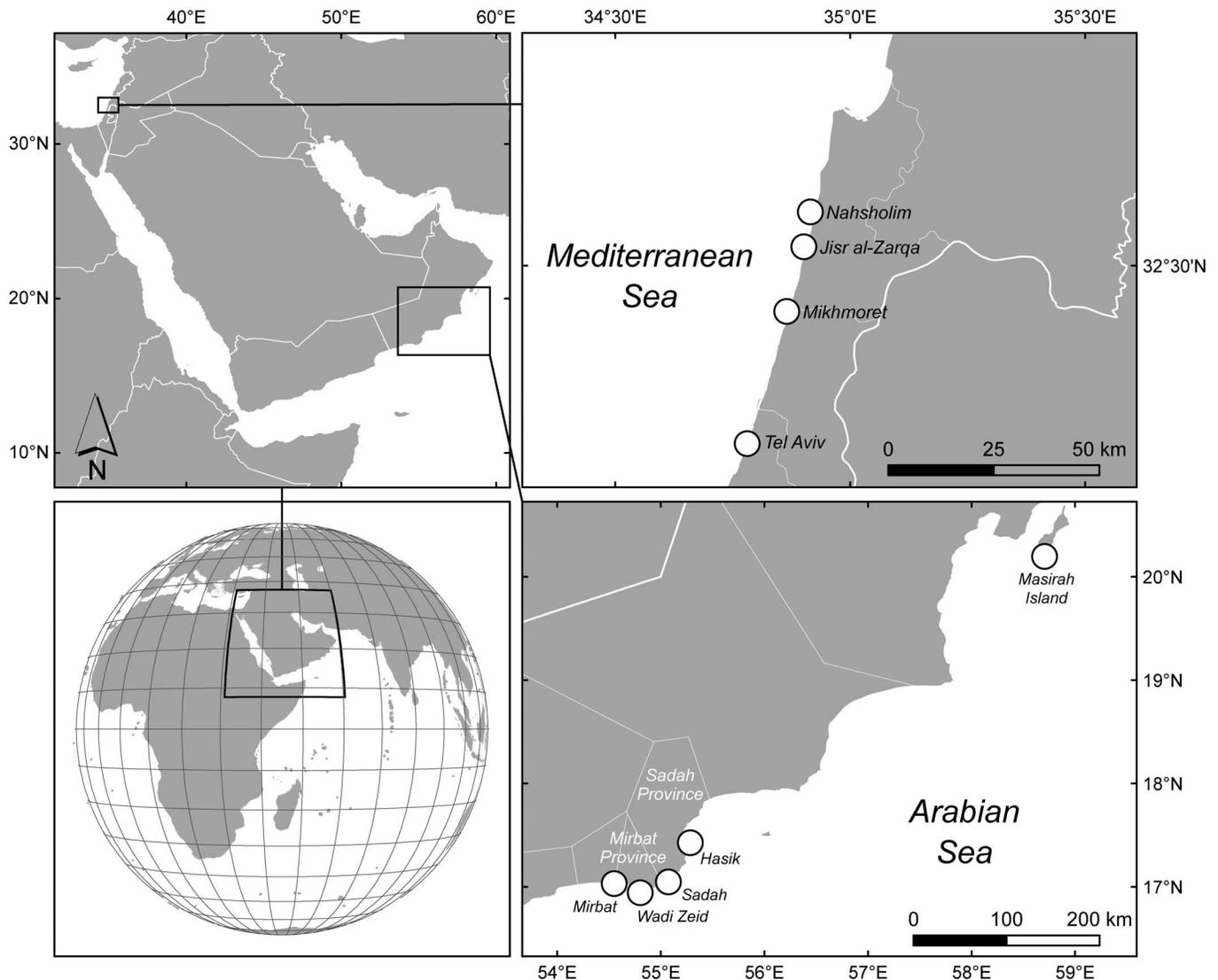


Fig. 1. Distribution range of *Codium pulvinatum* in Oman and Israel, with indication of the main collection sites.

The first dataset was analyzed with maximum likelihood in Randomized Axelerated Maximum Likelihood (RAxML) v.7.2.8 (Stamatakis 2006), using a general time reversible plus gamma (GTR + Γ) model of sequence evolution with separate parameter sets for the four partitions *rbcL* cp1-2, *rbcL* cp3, *rps3-rpl16* cp1-2, *rps3-rpl16* cp3. The choice of partitioning and model selection follows Verbruggen *et al.* (2012), who found this to be the best-fitting among 20 alternative strategies based on a virtually identical dataset. Statistical branch support was obtained by running 1000 replicates of traditional bootstraps (Felsenstein 1985).

The second dataset was analyzed with Bayesian Evolutionary Analysis Sampling Trees (BEAST; Drummond *et al.* 2012) and RAxML. For the BEAST analysis of this *rbcL*-only dataset, a Markov chain Monte Carlo (MCMC) of 10 million generations was run with an Hasegawa-Kishino-Yano plus gamma (HKY + Γ) model of sequence evolution partitioned as above (cp1-2, cp3). A relaxed clock model (uncorrelated log-normal) and coalescent tree prior (constant population size) were applied. Convergence was

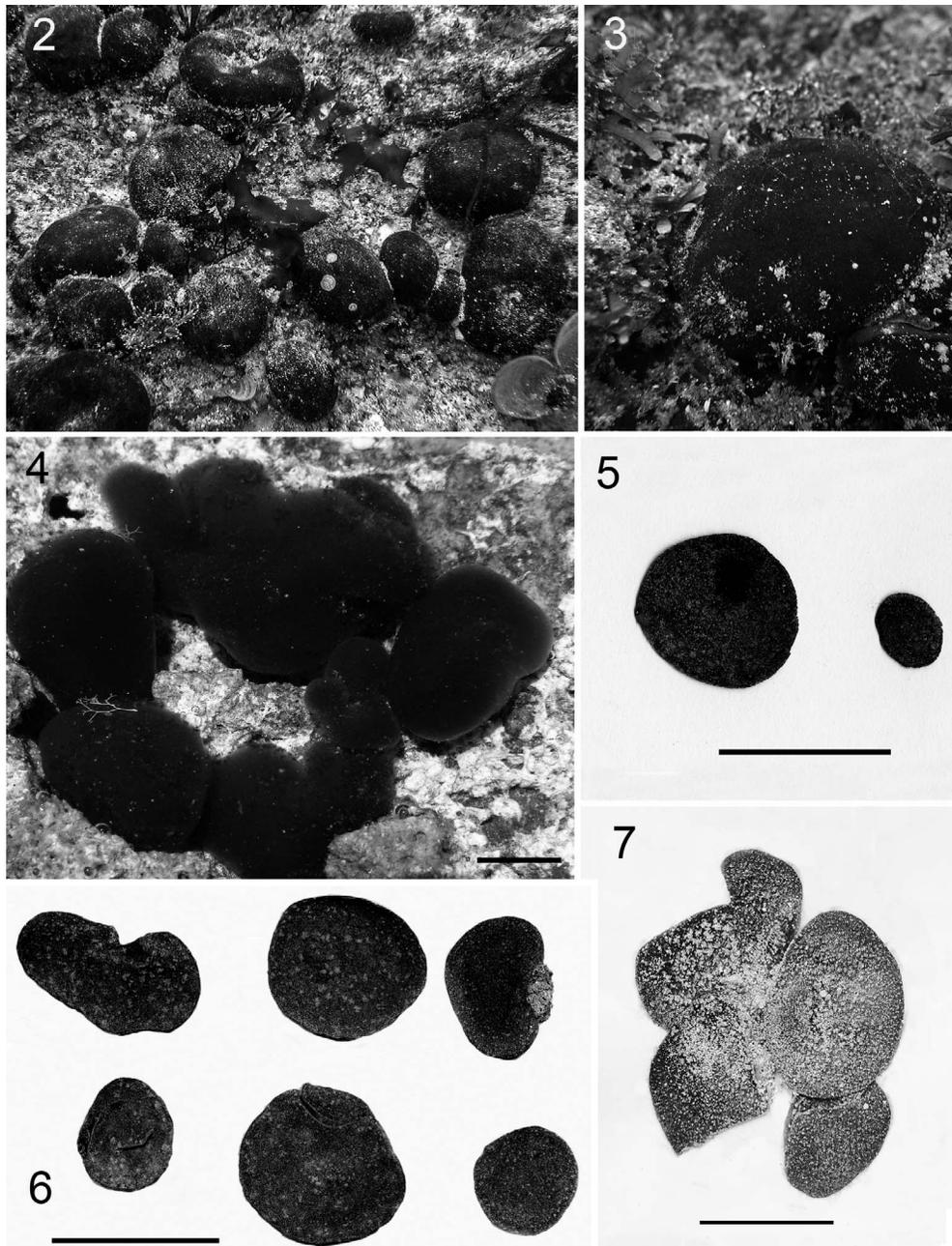
assessed from the trace files, and the MCMC was summarized using BEAST's accessory programs, discarding the first 10% of the run as burn-in. The RAxML analysis used the same model and partitioning and was run with 1000 rapid bootstrap replicates.

RESULTS

Codium pulvinatum M.J.Wynne & R.Hoffman *sp. nov.*

Figs 2–13

DIAGNOSIS: Thalli with a pulvinate to globose or subglobose habit, spongy, loosely attached to the substrate, which was typically rock surfaces; adjacent thalli becoming aggregated into larger masses; individual thalli 0.5–2.0 cm high, 0.5–4.5 cm in diameter but forming larger masses when becoming aggregated; utricles cylindrical, 1600–2160 μm in length, 170–62 μm in diameter; filament (siphon) 65–90 μm in diameter; gametangia spindle-shaped, 325–378 μm in length, 57–65 μm diameter; hairs were absent. Occupying the lower intertidal zone to shallow-deep subtidal as well as in tidal pools.



Figs 2–7. *Codium pulvinatum* sp. nov., *in situ* images and pressed specimens.

Fig. 2. *In situ* population, at ‘The Wreck’, Mirbat, Oman.

Fig. 3. *In situ* specimen, at ‘The Wreck’, Mirbat, Oman.

Fig. 4. *In situ* specimens from Tel Aviv, Israel. TAU 1938. Scale bar: 1 cm.

Fig. 5. Holotype (MICH 724094). Scale bar: 3 cm.

Fig. 6. Pressed Omani specimens (MICH 724089). Scale bar: 5 cm.

Fig. 7. Pressed Omani specimen (DHO2 0188). Scale bar: 3 cm.

HOLOTYPE: designated here: MICH 724094 (Fig. 5), collected by M.J. Wynne 2000-04-40, 11 September 2000, Raaha (= Alto) Bay (16.95116°N, 54.81650°E), in drift, east of Mirbat, Dhofar, Oman.

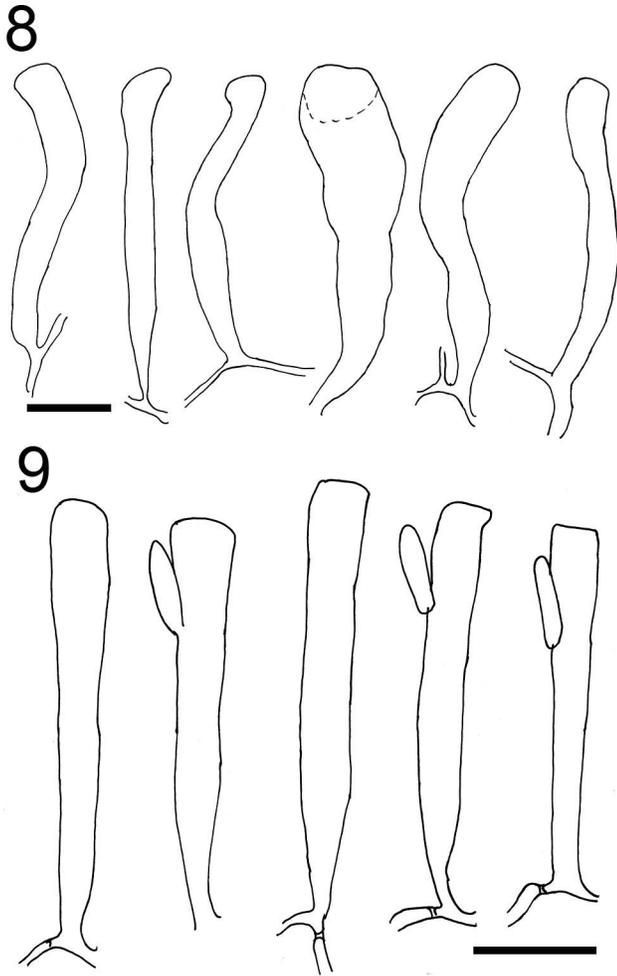
ISOTYPES: BM and ON.

PARATYPES: TAU1709, TAU1895, TAU1938, TAU1955, TAU1990, DHO 015, DHO2 0188. Others are listed in Table S1.

ETYMOLOGY: *pulvinatus*, Latin: cushion-shaped.

DISTRIBUTION: the Dhofar coast and Masirah Island of Oman (northern Arabian Sea); the central Mediterranean coast of Israel.

DESCRIPTION BASED ON OMANI AND ISRAELI SPECIMENS: Thalli usually occurred in scattered populations on hard or loosely consolidated substrates (Fig. 2). Individual thalli were spongy, light olive to dark green, globose (Figs 3–6) to lobed pulvinate and at times



Figs 8–9. *Codium pulvinatum* sp. nov. Camera lucida drawings of utricles, some with lateral gametangia.

Fig. 8. Utricles, Oman 2000-06-15. Scale bar: 500 µm.

Fig. 9. Utricles, some with lateral gametangia. Oman 2001-19-29. Scale bar: 500 µm.

formed multiple adjacent ball-like structures into a single structure (Fig. 7) attached to the substrate by tufts or rhizoidal filaments but not adherent. The thalli were up to 2 cm tall and up to 4 cm in diameter, loosely attached to substrate, and the medulla was filled by filaments or somewhat hollow. Utricles cylindrical or clavate, *c.* 5.6 times as long as broad, (730–) 1200–2220 (–2640) µm long, (140) 170–350 (–540) µm in diameter and their apices subtruncate to rounded with no thickenings (Figs 8, 9). Hairs were absent. Medullary filaments were (20–) 45–84 (–90) µm in diameter. Gametangia lance-ovoid or ampulliform (Figs 10, 11), *c.* 3.7 times as long as broad, (200–) 325–380 (–460) µm long, (55–) 65–100 (–165) µm in diameter. The ratios of averages of utricles/gametangia length and utricles/gametangia diameter were 4.2 and 3, respectively. Utricles carrying several gametangia (up to four) were often observed in specimens collected from Israel (Fig. 11), each borne on a short pedicel. Gametangia were also observed growing on filaments subtending utricles (Figs 12, 13).

The collecting trips in Oman were conducted almost entirely in the month of September, following the summertime monsoon season, and the several dozen specimens of *Codium pulvinatum* were collected both as attached and as drift specimens. Most of the hundreds of specimens of the

new species found in Israel were collected from the summer drift at sites located north of Tel Aviv (see map in Fig. 1 and Table S1). However, specimens collected from Nahsholim and Mikhmoret were found growing in caves and the shaded sides of potholes and rock pools located in the middle of the intertidal zone; whereas, in Tel Aviv (Fig. 1) specimens were also found growing in the shaded cracks between limestone rocks of wave breakers or even attached as epiphytes on *Codium taylorii* P.C.Silva growing in a cave between these rocks. Surveys of the Levantine shore of Israel revealed that this species starts growing in the beginning of summer (June) and fragments during summer and especially in autumn. It was not observed during winter and early spring, when surface seawater temperatures drop below 20°C.

Molecular results

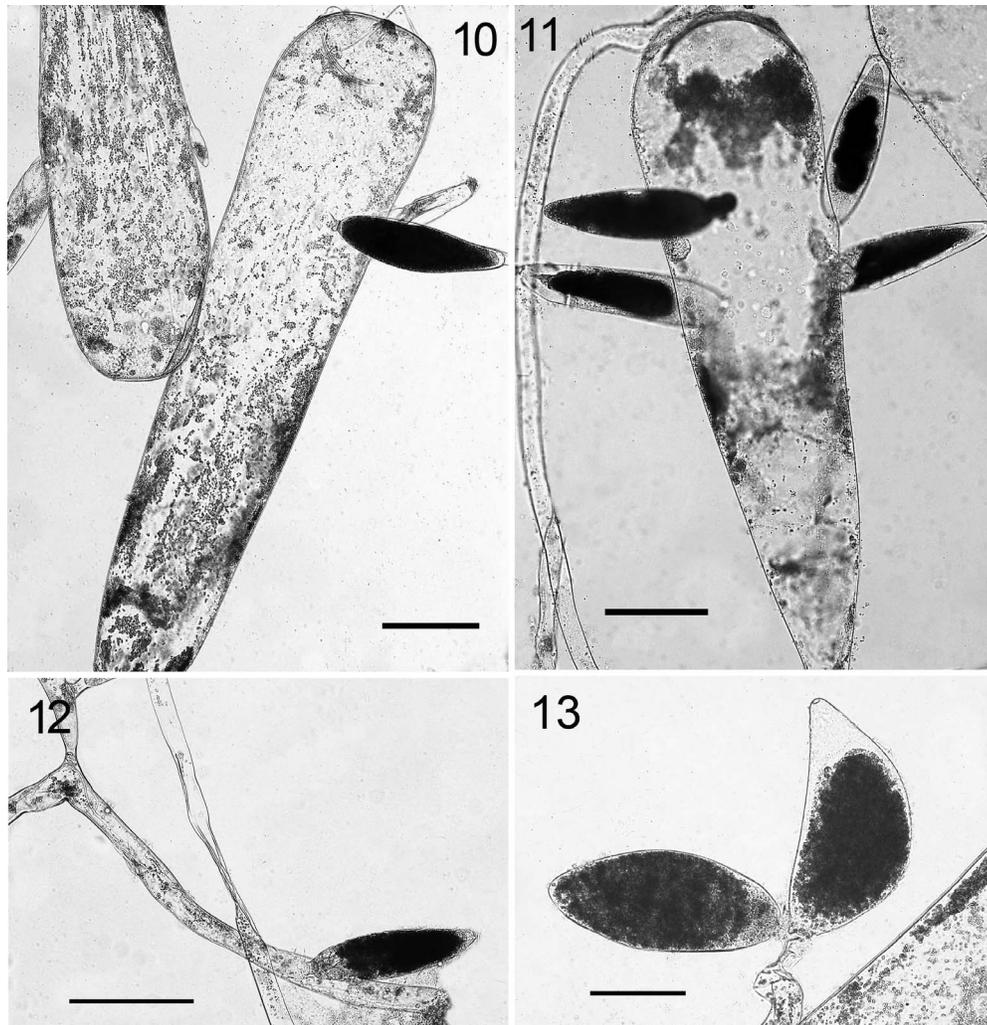
The phylogenetic tree inferred from concatenated *rbcL* and *rps3-rpl16* sequences (Fig. 14) showed that the target taxon was in a well-supported lineage with two other undescribed species from Oman, *Codium* cf. *latum* and *Codium* cf. *flabellatum*, consistent with previous phylogenetic studies, in which the target taxon was referred to as *Codium* cf. *minus* (Verbruggen *et al.* 2007, 2012; Oliveira-Carvalho *et al.* 2012; Huisman *et al.* 2015; Verbruggen & Costa 2015). It is important to note that while *C.* cf. *latum* and *C.* cf. *flabellatum* have morphological similarities to *C. latum* Suringar (Suringar 1867) and *C. flabellatum* Nizamuddin (Nizamuddin 2001), respectively, they are not closely related to them. In fact, these Omani species were clearly separated from genuine *C. latum* and *C. flabellatum* genetically (Fig. 15), and these names were only used to reflect morphological similarity.

The phylogeny also showed that *Codium pulvinatum* is not closely related to other ball-shaped species. The majority of ball-shaped species – generally with very large utricles – are found in the B2 clade (*C. megalophysum* P.C.Silva, *C. minus*, and *C. cranwelliae* Setchell included in this analysis). In clade C2, to which *C. pulvinatum* belongs, there are also the spherical *Codium ovale* and lobed *C. recurvatum* (arrowheads in Fig. 14) but these are not closely related to the target taxon.

The haplotype tree (Fig. 14) inferred from the dataset with multiple sequences per species showed that the genotypes of *C. pulvinatum* from Oman and Israel form distinct clusters. Within its supposedly native distribution range in Oman, *C. pulvinatum* haplotypes show a geographical differentiation between the adjacent Mirbat and Sadah (includes Hasik) provinces in the Dhofar Governate.

DISCUSSION

Codium pulvinatum is a common species along the southern shores of the Arabian Peninsula. Before it was recognized to be an undescribed species, it had gone under the mistaken identity of *C. ovale* (Schils & Coppejans 2003; Schils 2006; Schils & Wilson 2006) and of *C. minus* (Richards & Wynne 2003; Wynne 2004; Schils & Wilson 2006) because it has the same external morphology. Molecular data clearly show that *C. pulvinatum* is distinct at the species level (Fig. 15) and not closely related to either *C. minus* or *C. ovale* (Fig. 14). These three species are separated in phylogenetic trees, suggesting



Figs 10–13. Utricles of *Codium pulvinatum* sp. nov. with gametangia.

Fig. 10. Typical utricles bearing a lateral gametangium, Israeli collection. Scale bar: 200 μ m.

Fig. 11. Utricle bearing multiple gametangia. Israeli collection. Scale bar: 200 μ m.

Fig. 12. Gametangium produced on a siphon. Israeli collection. Scale bar: 200 μ m.

Fig. 13. Pair of gametangia produced on a siphon. Israeli collection. Scale bar: 100 μ m.

that their morphological resemblance was an instance of convergent morphological evolution (Verbruggen et al. 2007, 2012). The present study has demonstrated that its closest relationships in the genus are with two other Arabian Sea species that have upright morphologies.

A taxonomic account of *Codium* taxa with pulvinate to mamillate–globose habits was obtained from AlgaeBase (Guiry & Guiry 2017), the Macroalgal Herbarium Portal (<http://macroalgae.org/portal/index.php>; especially the collections at MICH and UC), and the taxonomic literature, which resulted in 21 species. We excluded the following taxa: *C. dimorphum* Svedelius, *C. hubbsii* E.Y.Dawson, *C. cerebriforme* Setchell in Skottsberg, *C. coralloides* (Kützing) P.C.Silva, *C. lucasii* subsp. *capense* P.C.Silva, *C. pomoides* J.Agardh and *C. effusum* (Rafinesque) Delle Chiaje from the comparison presented in Table 1. Despite having a comparable overall external morphology to *C. pulvinatum*, these species differ in the lower parts of their thalli, which are usually strongly

adherent and tightly attached to the substrate (Svedelius 1900; Setchell & Gardner 1903, 1920; Setchell 1937; Dawson 1950; Silva 1951; Silva & Womersley 1956; Silva 1959; Scagel 1966; Womersley 1984; Hoffmann & Santelices 1997; Pedroche et al. 2002; Silva & Chacana 2005; Rodríguez-Prieto et al. 2013; Cormaci et al. 2014). *C. coralloides* and *C. effusum* are regarded as native species in the Mediterranean Sea. *C. recurvatum* was also omitted because it has flattened lobes originating from a central holdfast and curving back toward the substratum (Verbruggen et al. 2012). Table 1 presents a comparison of morphological characteristics of the remaining 13 species and *C. pulvinatum* specimens from Oman and Israel. Table 1 indicates that *C. minus*, *C. bursa* (Olivi) C.Agardh, *C. cranwelliae*, *C. globosum* A.H.S.Lucas, *C. mamillosum* Harvey, *C. spongiosum* Harvey, *C. elisabethiae* O.C.Schmidt, *C. megalophysum* and *C. papenfussii* P.C.Silva have utricles that are significantly longer and sometimes wider than those of *C. pulvinatum*. On the other hand, *C. ovale* and *C. saccatum*

Table 1. Morphological comparison of *Codium* taxa that have pulvinate to mamillate–globose habit.

Characters	<i>Codium pulvinatum</i> (Oman)	<i>Codium pulvinatum</i> (Israel)	<i>Codium ovale</i>	<i>Codium minus</i>	<i>Codium bursa</i>
Vegetative characters					
General morphology					
Habit	pulvinate to subglobose, lobed, adjacent thalli becoming aggregated, not firmly attached	subglobose to pulvinate, a bit lobed, at times forming multiple adjacent ball-like structures into a single structure	spherical	pulvinate, spherical to kidney-shaped; globose to more or less depressed globose	spherical or subglobose
Height–length (cm)	1.0–2.0	0.5–2	0.5–3		
Diameter-wide (cm)	1–4.5	0.5–3.5	0.6–3	2–3	1–40
Utricles					
Shape	clavate to cylindrical	clavate to cylindrical	clavate to cylindrical	clavate, subtruncate or slightly rounded at apex	clavate
Length (µm)	1600–2160	(730–)1560(–2640)	(470–)635(–1200)	3000–3500 (–5000)	up to 4500
Diameter (µm)	170–262	(140–)280(–540)	(155–)280(–400)	(300–)400–700(–800)	250–550
Hair/Scar (present, absent)	absent	absent	present	absent	present
Filament diameter (µm)	65–90	(20–)45(–84)	26–75		
Reproductive characters					
Gametangia morphology	spindle-shaped	spindle-shaped	spindle-shaped, elongated oval	narrowly ellipsoid to ovoid	spindle-shaped or ovoid
Length (µm)	325–378	(200–)380(–460)	250–400		
Diameter (µm)	57–65	(55–)100(–165)	54–116		
Comments	apices of utricles with no thickening	loosely attached to substratum by tufts or rhizoidal filaments		1–3 gametangia/utricle	
References	Verbruggen <i>et al.</i> (2012); this study	this study	Schmidt (1923); Van den Heede & Coppejans (1996); Littler & Littler (2000)	Schmidt (1923); Kim & Klochkova (2010)	Maggs & Kelly (2007); Rodriguez-Prieto <i>et al.</i> (2013); Cormaci <i>et al.</i> (2014)

Okamura have smaller and shorter utricles. This difference is obvious in the latter species, which has the shortest utricles of all species studied. *C. perrinae* A.H.S.Lucas and *C. ritteri* Setchell & N.L.Gardner have utricles that are in the length and diameter size ranges of *C. pulvinatum*; however, the utricles in those two species are characterized by thickened apices; whereas, hundreds of utricles studied in the dozens of specimens collected in Oman and Israel clearly show that apices of the utricles of the new species are simple with no thickening or extra features and are lacking hairs.

The distribution range of *C. pulvinatum* throughout the Arabian Seas is currently unclear. Past records of *Codium* from the Red Sea do not readily indicate that the species

might occur there. Papenfuss (1968) listed a total of five *Codium* species for the Red Sea; although, he doubted the records of *C. tomentosum* Stackhouse. Only *C. arabicum* Kützing approaches the habit of *C. pulvinatum* but the habit of *C. arabicum* is lobed and tightly adherent (Kützing 1856; Børgesen 1940, 1948; Hoffman *et al.* 2011), not pulvinate or globose. *C. parvulum* (Bory) P.C.Silva was later reported for the Red Sea by Silva (Silva & Lipkin 2003). The habit of that species, however, consists of many ramified, terete, repent axes.

The observation that *C. pulvinatum* in Israel mainly occurs in shaded habitats corresponds to its subtidal growth in seasonally turbid seas along the upwelling shores of the

Table 1. Extended

<i>Codium spongiosum</i>	<i>Codium elisabethiae</i>	<i>Codium megalophysum</i>	<i>Codium papenfussii</i>	<i>Codium ritteri</i>
prostrate, pulvinate or applanate, with undulate to cerebriform lobes	globose or subglobose	globose or hemispherical, gregarious	hemispherical, subglobose to cerebriform	globose to pyriform, spongy, prostrate
14 (–50)	up to 14	up to 10	2–7 (–12)	3–4 1–2 (–10)
cylindrical or clavate	subcylindrical to slightly clavate	cylindrical, clavate, knobby or mammiform outgrowths in the upper half	cylindrical or slightly clavate, in small clusters	clavate, blunt
(1500–)2800–3300 (–6000) (130–)275–400(–620)	(2500–)3000–5500 (–6700) 265–530	5000–12,000 (1000–)1500–2700 (–3900)	(2400–)3000–4600 (–5400) (300–)330–520(–680)	1800–2500(–4000) 150–400 (–800)
present	present	absent	absent	
30–100	60–110–130	215–430	50–110	45–60
lance-ovoid or ampulliform	narrowly ellipsoidal to cylindrical, usually tapered anteriorly	ellipsoidal, ovoid or ampulliform, several per utricle, 2000–3500 mm below apex of utricle	lance-ovoid, one or two per utricle, c. 1 mm below apex	
215–360 50–175	370–550 65–130	540–1030 190–380	480–590 155–220	
loosely adherent to substratum, apices thickened	second utricle being produced directly from the parent utricle	loosely attached to substratum, has huge loosely grouped utricles	loosely attached to substratum, utricles with a typical prominent bulge	utricles' tips thickened
Silva & Womersley (1956); Jones & Kraft (1984); Kraft (2007)	Schmidt (1929); Guiry & Guiry (2017)	Silva (1959); De Clerck <i>et al.</i> (2005)	Silva (1959); De Clerck <i>et al.</i> (2005)	Setchell & Gardner (1903, 1920); Scagel (1966)

Arabian Peninsula (Schils & Coppejans 2003). Surveys of the Levantine shore of Israel, conducted throughout the years, revealed that *C. pulvinatum* grows in summer and fragmentation occurs in summer but we did not observe this species anywhere during winter. The first three specimens collected from the Mediterranean were found at Mikhmoret on 24 October 2014. This site has been monitored regularly for the past 15 years, and the intertidal pool where the first records were collected has been surveyed four times per year since 2002, without any prior record of a *C. pulvinatum* look alike. Since 2014, hundreds of samples were collected of thousands observed along the northern shore of the city of Tel Aviv, where this species occurs in high population densities.

Therefore, it is speculated that *C. pulvinatum* is a new invasive species for the Mediterranean Sea, which reached Tel Aviv in the past 5 years and spread quickly by means of the northward currents to other central Israeli shores. The vector of introduction of *C. pulvinatum* into the Levantine Sea is uncertain.

We postulate that *Codium pulvinatum* has reached the Levantine shores of Israel through Lessepsian Migration. Based on the observation that the Israeli specimens were not nested or intermixed with the Omani ones, it can be assumed that the source population of the invasive haplotypes originates from another location in the species' native distribution range within the Arabian Sea or the Red Sea.

Table 1. Extended

<i>Codium cranwelliae</i>	<i>Codium globosum</i>	<i>Codium perrinae</i>	<i>Codium saccatum</i>	<i>Codium mamillosum</i>
prostrate, spongy, domed cushions	globose, solid, attached to substratum by 'silky threads'	globose to pulvinate sometime lobed, crescent or even ring-shaped	subspherical to fluted in contour, entire or 1–4 times perforated, solitary or in loose clusters	globular, oval, obovoid, depressoglobular, transversely oblong
			0.8–9(–13)	1–2
to 12	1–2	12	1–18(–22)	1–7
		oblong cylindrical or ovoid, apical wall moderately to markedly thickened into a lamellate galeate cap to 56 µm thick	short, oblong or subcylindrical, a little swollen laterally at apex	club-shaped and elongated, gradually tapering below, subtruncato-roundish and thickened walled at apex, up to 40 µm
	3000	920–1700	both types 200–300	(–3000)4000–7000(–9000)
	275–350	130–240(–375)	120–230 (primary) 40–90 (secondary)	(400–)450–1000(–1500)
absent		absent	present	absent
	30	26–60	10–15	40–105
	not observed	fusiform to subcylindrical, borne 540–630 µm below apex of utricle	pyriform, bilanceolate to linear	narrowly ellipsoid or ampulliform, 1–3 per utricle
6000		370–450 65–100	120–140 (–160) 50–80	(390–)520–780 130–250
hairs absent	utricles bluntly obtuse		hairs infrequent	
Adams (1994)	Lucas (1927)	Lucas (1935); Silva & Womersley (1956)	Okamura (1915); Kraft (2007)	Okamura (1915); Schmidt (1923); Silva & Womersley (1956)

Lessepsian Migration of algal species from the Red Sea into the Mediterranean Sea has been well documented (Aleem 1948, 1950, 1984).

Four other alien *Codium* taxa have been reported from the Mediterranean Sea thus far. *C. fragile* (Suringar) Hariot subsp. *fragile* established large populations in the western and central Mediterranean; whereas, *Codium taylorii*, *Codium arabicum* and *Codium parvulum* invaded the Levantine Sea and became invasive (Hoffman *et al.* 2011; Hoffman 2014; Verlaque *et al.* 2015). The addition of the new invasive *Codium* to the other three species above may point to high tolerance of this genus to environmental factors that characterized the Levant Mediterranean shore.

Global warming and the rise of surface seawater temperatures in the Levantine Sea probably paved the way to the establishment of these four tropical species.

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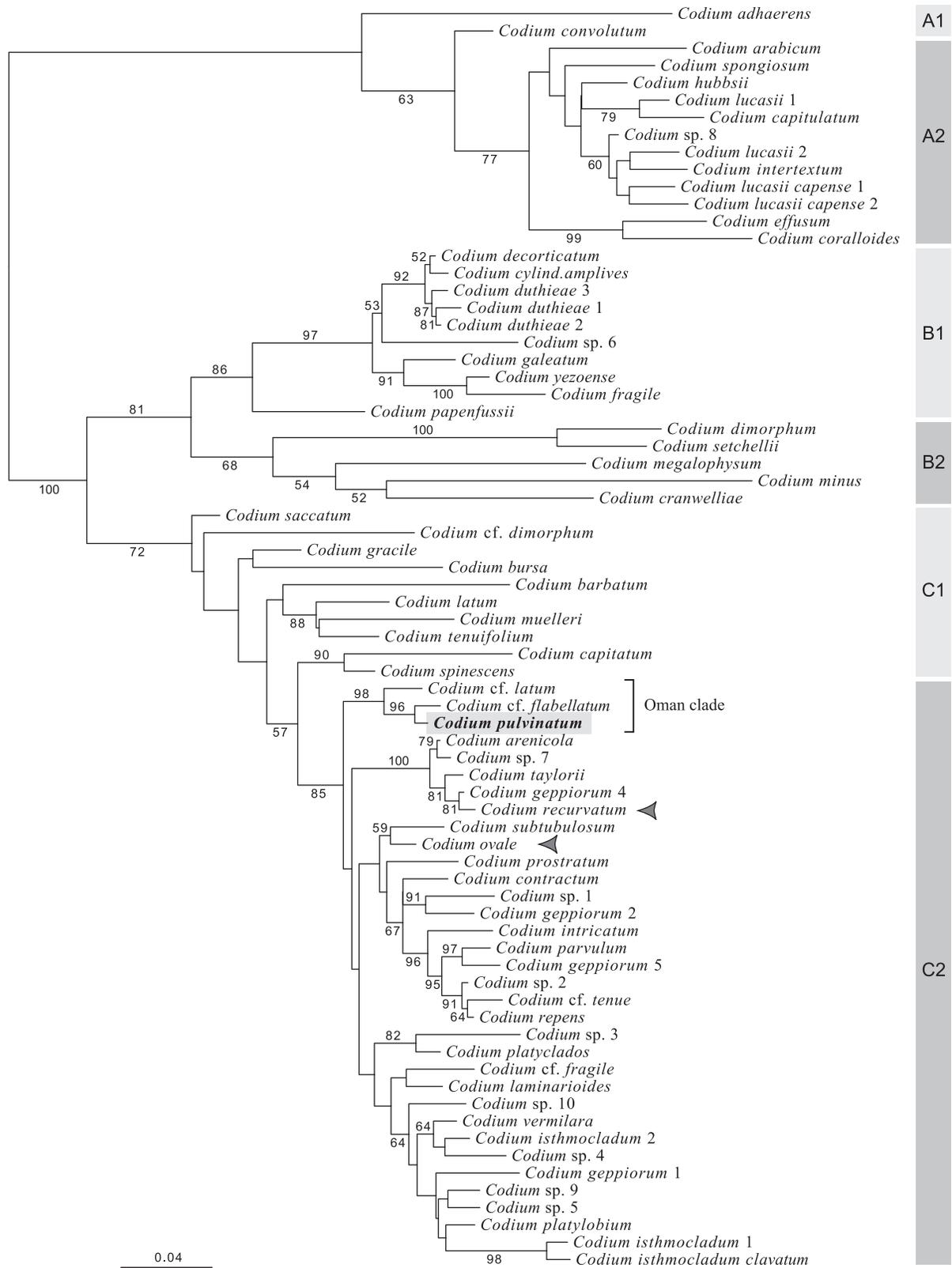


Fig. 14. Phylogenetic tree of *Codium* species inferred from concatenated *rbcL* and *rps3-rp16* sequences with maximum likelihood. The scale is in estimated substitutions per site, and bootstrap support values exceeding 50 are plotted on the branches. The new species is shown in a grey box.

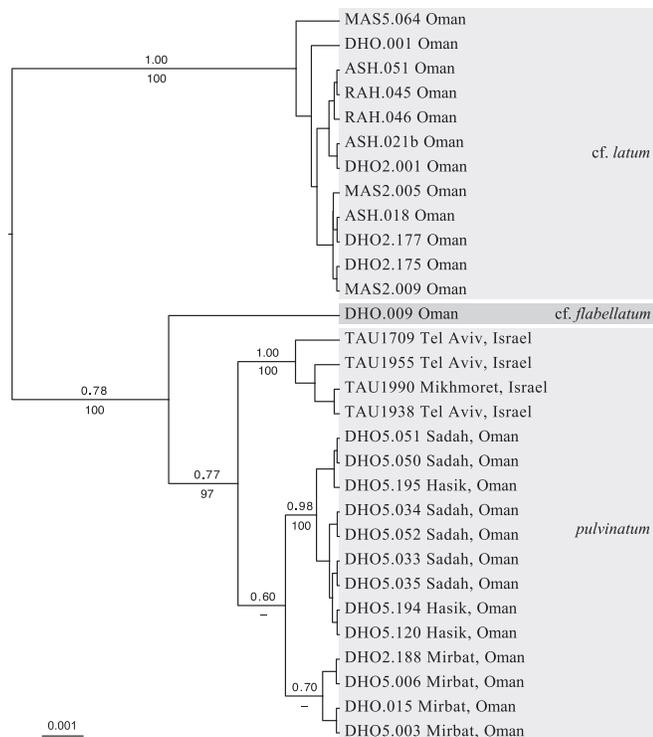


Fig. 15. Haplotype tree of *rbcL* sequences of *Codium pulvinatum*, *C. cf. flabellatum* and *C. cf. latum*. The tree is inferred with BEAST using a coalescent prior, so non-zero branch lengths result even when sequences are identical. Support values are shown only for the main branches and are given as Bayesian posterior probabilities (above branches) and ML bootstrap values (below branches).

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.2216/17-74.1.s1>.

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