



Re-examination of the distribution and species diversity of the genus *Padina* (Dictyotales, Phaeophyceae) in the Mediterranean Sea

ILARIA PAGANA*, GENNY MARROCCIA, GIULIANA MARLETTA & GIUSEPPINA ALONGI

Department of Biological, Geological and Environmental Sciences, University of Catania, Via Empedocle, 58, Italy

✉ ilaria.pagana@phd.unict.it; <https://orcid.org/0000-0003-3612-9079>

✉ genny.marroccia@gmail.com; <https://orcid.org/0009-0006-8917-9706>

✉ giulianamarletta93@gmail.com; <https://orcid.org/0000-0003-4602-8036>

✉ g.alongi@unict.it; <https://orcid.org/0000-0003-2604-6106>

*Author for correspondence

Abstract

This study aimed to expand knowledge on the distribution and biodiversity of the genus *Padina* in Sicily and in the Mediterranean Sea. Thanks to the studies of samples collected along the Sicilian coast and the re-examination of herbarium specimens labelled as *Padina pavonica*, we reported the following five species in Sicily: *P. ditristromatica*, *P. gymnospora*, *P. pavonica*, *P. pavonicoides* and *P. tetrastromatica*. Particularly, we documented the first supported occurrence of *P. gymnospora* in the Mediterranean Sea and the first finding of *P. pavonicoides* and *P. tetrastromatica* along the Italian coast. Furthermore, a new key was created for the identification of all species belonging to the genus *Padina* present in the Mediterranean Sea today.

Key words: Identification keys, Marine macroalgae, Phytobenthos, Sicily, Taxonomy

Introduction

The genus *Padina* Adanson (1763) includes about 60 species (Guiry and Guiry, 2023), and approximately one-half occur in temperate and tropical regions where they are found from the lower intertidal to the subtidal (Ni-Ni-Win *et al.* 2011a, Arraj *et al.* 2016). According to Silberfeld *et al.* (2013) and Vieira *et al.* (2021), the genus *Padina* exhibits a high specific diversity whose rate of diversification remains constant over time furthermore, cryptic species and inaccurate identifications have also been detected.

Species of the genus *Padina* show thalli attached by a rhizoidal holdfast, are characterised by complanate/flabelliform laminae often lacerated that show low or heavy calcification and pheophytic hairs in tufts arranged along concentric lines on one or both blade surfaces (Cormaci *et al.* 2012). The rolled margin consists of meristematic cells, from which growth begins, and is always composed of 2 layers of cells, which can increase in number almost immediately. The number of cell layers of the blade in the basal and median part changes from one species to another, therefore this number may be another essential diacritical character for the taxonomy of the genus *Padina* (Ni-Ni-Win *et al.* 2011a).

The species belonging to this genus have an isomorphic haplodiplophase digenetic life cycle; the sporophytes with the unilocular cysts (tetrasporocysts) grouped in rows/concentric zones on one or both surfaces and, the gametophytes are rather rare, with oocysts and antheridia arranged in sori in concentric zones (Ni-Ni-Win *et al.*, 2011b). The sori may be covered by a thin membrane, called *indusium*, which prematurely breaks (Ni-Ni-Win *et al.* 2011a, Cormaci *et al.* 2012). Finally, some species may present a *Vaughaniella* stage (creeping rhizomes), consisting of a small ribbon-like thallus with a single apical cell (Børgesen 1951, Cribb 1951, Umezaki & Yoneda 1962, De Clerck & Coppejans 1997).

In Mediterranean Sea, a total of seven species were reported: *Padina boergesenii* Allander & Kraft (1983: 87) [(also as *P. gymnospora* (Kützting) Vickers non Sonder], *P. boryana* Thivy (in Taylor 1966: 355), *P. ditristromatica* Ni-Ni-Win & H. Kawai (in Ni-Ni-Win *et al.* 2011a: 333), *P. pavonica* (Linnaeus) Thivy (in Taylor 1960: 234), *P. pavonicoides*

Ni-Ni-Win & H. Kawai (in Ni-Ni-Win *et al.* 2011a: 335), *P. tenuis* Bory (1827: 590), and *P. tetrastromatica* Hauck (1887: 43–44) (Tsekos & Haritonidis 1977, Ribera *et al.* 1992, Cecere *et al.* 1996, Barceló *et al.* 1998, Furnari *et al.* 1999, 2010, Rindi *et al.* 2002, Mayhoub 2004, Serio *et al.* 2006, Gómez-Garreta *et al.* 2007, Bitar *et al.* 2017).

Among these, *P. tenuis* is considered a misidentification of *P. boergesenii* by Ni-Ni-Win *et al.* (2011a), while Cormaci *et al.* (2012) point out that the report of *P. boryana* is poorly supported and that the only ascertained species occurring at the Mediterranean Sea are: *P. ditristromatica*, *P. pavonica* and *P. pavonicoides*. However, they did not consider *P. tetrastromatica*, reported instead by Mayhoub (2004) for Syria, and further stated that *P. boergesenii* is also a misidentification, according to Ni-Ni-Win *et al.* (2011a); the latter Authors, indeed, assert that they are unable to determine whether this report is correct, whether it is a misidentification or whether it refers to one of their new species in the absence of morphological observations (Ni-Ni-Win *et al.* 2011a). Subsequently, findings of *P. boergesenii* in the Levantine basin of the Mediterranean were reported (Bitar 2017). Finally, regarding *P. boryana*, its presence was documented by Arraj *et al.* (2016) in the eastern Mediterranean using morphological and anatomical characteristics.

Therefore, to date, the species assumed to be present in the Mediterranean Sea are the following: *P. boergesenii*, *P. boryana*, *P. ditristromatica*, *P. pavonica*, *P. pavonicoides*, *P. tetrastromatica*.

Since in the past, due to the morphological similarity between species belonging to the genus *Padina*, misidentifications of these taxa have often been made, a re-examination of the old records labelled as *P. pavonica* (the species thought to be most common in the Mediterranean) and the study of new samples, could lead to a new delineation of the distribution areas of the species of this genus in the Mediterranean Sea. According to this, the present work aims to enrich the knowledge of the biodiversity of the genus *Padina* in this geographic area, through the study of collected samples around the Sicilian coasts, the re-examination of *herbarium* specimens and the creation of an identification key to the species belonging to this genus and present in the Mediterranean Sea today.

Methods

Throughout 2021 and 2022, 15 populations of *Padina* specimens were investigated in the infralittoral zone in some localities of Sicily (Table 1, Fig.1), and for each population, 3/5 thalli were collected for morphological analysis. The collected material was stored in silica gel (to prevent formaldehyde transport) to later perform a study in the Laboratory of Phycology of the Department of Biological, Geological and Environmental Sciences of the University of Catania. In addition, we revised 13 *herbarium* sheets labelled as *P. pavonica* that were held in CAT *Sectio Algae-Herbarium exiccata* of the University of Catania; as many thalli as possible, for each *herbarium* sheets, were analysed morphologically. Details on the species investigated are resumed in Table 2. For the anatomical and morphological observation, all thalli were rehydrated and the sections in the basal (close to rhizoids), median, and rolled apical portions were made by hand with the razor blade. The diacritical characters that have been used for species identification are (Table 3): i) the presence or absence of calcification on the two thallus surfaces; ii) the amount, the structures, and the arrangement of hair lines on the thallus surfaces; iii) the layers of cells in the apical rolled portion, in the median, and basal portion; iv) the structures and the arrangement of sporangial sori; v) the presence or absence of the *indusium*; vi) the present or absence of *Vauganiella* stage. We considered the lower surface to be the outer or convex surface, while we considered the upper (inner or concave) surface to be the one on which the upper edge is rolled. Photographs were taken with a Nikon D40 and processed using Adobe Photoshop 6.0. The map showing the sampling sites (Fig. 1) was realised through the QGIS software 3.16.

TABLE 1. Sampling sites of *P. ditristromatica*, *P. gymnospora*, *P. pavonica*, *P. pavonicoides* and *P. tetrastromatica*.

<i>eastern coast of Sicily</i>		
Aci Trezza (CT)	37°33'41"N; 15°9'59"W	–0.5; –5
Brucoli (SR)	37°17'25"N; 15°11'53"W	–0.5; –9.5
Penisola Magnisi (SR)	37°9'00"N; 15°13'59"W	–0.5; –5
Santa Tecla (CT)	37°38'24"N; 15°11'03"W	–0.5; –9.5; –13.4; –23.9

.....continued on the next page

TABLE 1. (Continued)

<i>northern coast of Sicily</i>		
Milazzo (ME)	38°14'40"N; 15°14'28"W	-0.5 m; -5m
Filicudi (Eolian Island)	38°33'27"N; 14°34'15"W	-0.5 m; -5m
<i>western coast of Sicily</i>		
Punta Raisi (PA)	38°11'24"N; 13°7'24"W	-0.5m;
Macari (TP)	38°8'15"N; 12°44'9"W	-0.5m;
<i>south of Sicily—Pantelleria</i>		
Cala Tramontana	36°47'54"N; 12°2'52"W	-0.5 m; -5m
Kattibuale	36°49'21"N; 11°59'11"W	-0.5 m; -5m
Martingana	36°44'56"N; 12°2'43"W	-0.5 m; -9.5m
Scauri	36°46'10"N; 11°57'48"W	-0.5 m; -5m; -9.5m

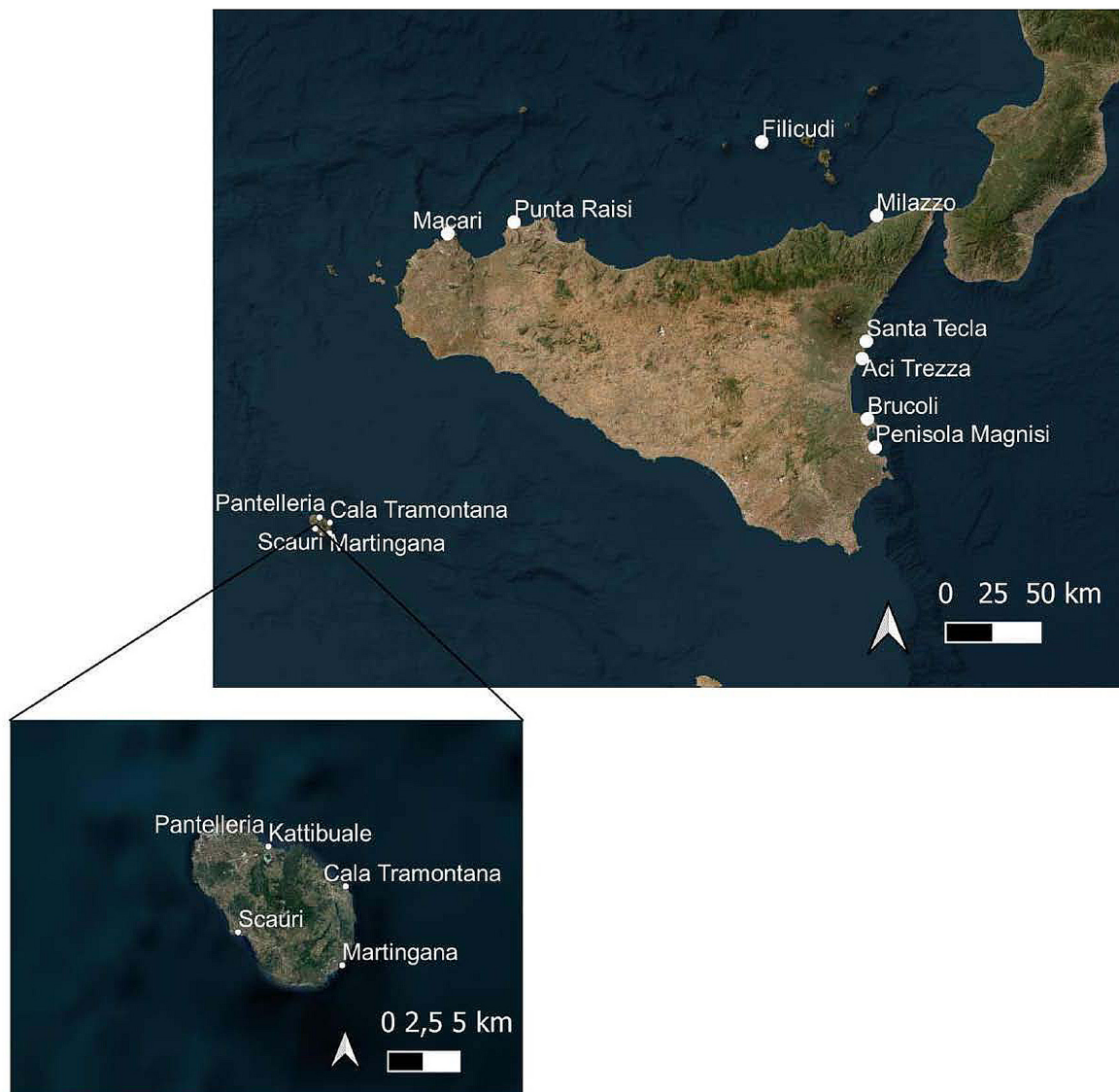


FIGURE 1. Maps of Sicily showing the sampling sites. Design by I. Pagana.

TABLE 2. *Herbarium* sheets examined.

	Herbaria code	Collection date	Collection site	Depth	Legit/Determinavit
<i>P. ditristromatica</i>	CAT1110	27/07/1969	Marzamemi	–2m	Scammacca/Scammacca
<i>P. gymnospora</i>	CAT 1735	2/1/1967	Palma di Montechiaro	–0.5 m	- / Giaccone
	CAT1733	05/09/1970	Pantelleria Island	–5 m	Giaccone / Giaccone
	CAT1734	05/09/1970	Pantelleria Island	–5 m	Giaccone / Giaccone
	CAT1104	25/01/1970	Brucoli	–0,5 m	Scammacca / Scammacca
	CAT1732	04/07/1967	Ustica	–10 m	- / Giaccone
<i>P. pavonica</i>	CAT1729	18/05/1969	Lipari Island	–4 m	Giaccone / Giaccone
	CAT1111	29/07/1968	Gela	–0,5 m	Scammacca / Scammacca
	CAT1722	18/10/1966	Palma di Montechiaro	–1 m	- / Giaccone
	CAT1728	04/04/1969	Capo Milazzo	–4 m	Giaccone - Giaccone
	CAT1727	07/06/1969	Capo Zafferano	–8 m	- /Giaccone
	CAT1096	12/06/1970	Syracuse	–0,5 m	Scammacca / Scammacca
<i>P. tetrastromatica</i>	CAT 1730	4/5/1966	Punta Raisi	–2m	/Giaccone

Results

Based on the diacritical characters, resumed in Table 3, the samples studied were identified as *P. ditristromatica*, *P. gymnospora* (Kützing) Sonder (*non* Vickers), *P. pavonica*, *P. pavonicoides*, and *P. tetrastromatica*.

The following information is given for each species: basionym, type locality, distribution in the Mediterranean Sea, examined specimens, brief morphological description, and remarks on species.

Padina ditristromatica (Fig. 2 A–E)

Basionym:—*Padina ditristromatica*

Type locality:—ITALY. Syracuse: Brucoli, Augusta

Distribution in the Mediterranean Sea:—GREECE (Ni-Ni-Win *et al.* 2011a, Catra & Alongi 2013, Tsiamis *et al.* 2013). ITALY (Ni-Ni-Win *et al.* 2011a, Bottalico *et al.* 2016). SPAIN (Gómez Gómez *et al.* 2015). SYRIA (Arraj *et al.* 2016). TURKEY (Ni-Ni-Win *et al.* 2011a).

Examined Specimens:—ITALY. Catania: Santa Tecla, Acireale, –13.4m, –23.9m, 02/07/2021; ITALY. Syracuse: Marzamemi, –2m, 27/07/1969, CAT1110 as *P. pavonica*.

Morphology:—the *thallus* is flabelliform and subdivided into lobes (Fig. 2A). It is fixed to the substrate through a tangle of fibrous rhizoid filaments, which cover the lower surface of the basal portion (Fig. 2A). This species has calcified striae on both surfaces, except on the hair lines. The latter, concentrically arranged, are alternate on both surfaces and are spaced unequally (Fig. 2B), they are also narrow-undepressed on the upper surface and broad-depressed on the lower surface. The rolled part of the apical portion shows 2 layers of cells (Fig. 2C), while the median and basal portions feature a mixture of 2–3 cell layers, since some cells divide transversally (Fig. 2D, E). In the 2-layered region, the cells of the upper side are twice as high as those of the lower side (Fig. 2C), while in the 3-layered region portion, all three layers show the same height (Fig. 2D, E). In our samples, no reproductive traits were found.

Remarks:—this species was described by Ni-Ni-Win *et al.* (2011a) on specimens collected at Brucoli (eastern coast of Sicily) and after that, there have been no further reports along the Sicilian coasts. Our records extend the distribution range also in areas contiguous to the type locality both northward (Santa Tecla-Acireale) and southward (Marzamemi—Syracuse); in particular, the latter is based on the re-examination of the *herbarium* sample from 1969, labelled as *P. pavonica*.

Although *P. ditristromatica* has been reported both in the eastern and western Mediterranean basin, it is very likely that this species may have a wider distribution throughout the Mediterranean Sea, due to a possible misidentification with *P. pavonica*.

TABLE 3. Morphological and reproductive characters of *P. ditristromatica*, *P. gymnospora*, *P. pavonica*, *P. pavonicoides* and *P. tetrastromatica*. 1 this paper; 2 Abbas & Shameel (2013a); 3 Abbas & Shameel (2013b); 4 Aisha & Shameel (2010); 5 Cormaci *et al.* (2012); 6 Gaillard (1967); 7 Gómez Gómez *et al.* (2015); 8 Huisman (2015); 9 Ni-Ni-Win *et al.* (2011); 10 Ni-Ni-Win *et al.* (2013); 11 Peralta (2013); 12 Womersley (1987)

Characters	<i>Thallus surface</i>	<i>P. ditristromatica</i> 5, 7, 9	<i>P. gymnospora</i> 2, 3, 12	<i>P. pavonica</i> 1, 5, 7, 9, 11	<i>P. pavonicoides</i> 1, 5, 7, 9	<i>P. tetrastromatica</i> 3 as <i>P. antillarum</i> , 4, 6, 8, 10
Calcification	<i>upper</i>	heavy	light	light	light	light
	<i>lower</i>	moderate	absent	absent or light	absent or light	absent
Hair lines	<i>upper</i>	conspicuous	inconspicuous	inconspicuous	inconspicuous	inconspicuous
	<i>lower</i>	conspicuous	conspicuous	moderate	moderate	conspicuous
Arrangement of hair lines between the two surfaces		unequal distance	equal distance	equal distance	equal distance	equal distance
		narrow-undepressed	not prominent	narrow-undepressed	narrow-undepressed	narrow-undepressed
Structures of hair lines	<i>upper</i>	broad-depressed	not prominent	narrow-undepressed	broad-slightly depressed	narrow-undepressed
	<i>lower</i>	narrow-undepressed	not prominent	narrow-undepressed	narrow-undepressed	narrow-undepressed
Layers of cells	<i>rolled apical portion</i>	2	2	2	2	2
	<i>median</i>	mixture 2 - 3	3 - 4	3	3	3 - 4
	<i>base</i>	mixture 2 - 3	6 - 8	3 - 4	3	4
Position of sporangial sori	<i>upper</i>	absent	present	absent	absent	absent
	<i>lower</i>	present	present	present	present	present
Structures of sporangial sori		narrow	-	broad above hair lines, narrow below hair lines	narrow	broad
		broken lines or patches above hair lines	more or less continuous lines	continuous lines on both sides of the hair lines	patches above hair lines	continuous lines above hair lines, discontinuous lines below the hair lines
<i>Indusium</i>		present	absent	present	present	absent
<i>"Vaughaniella"</i> stage		absent	-	present	present	present

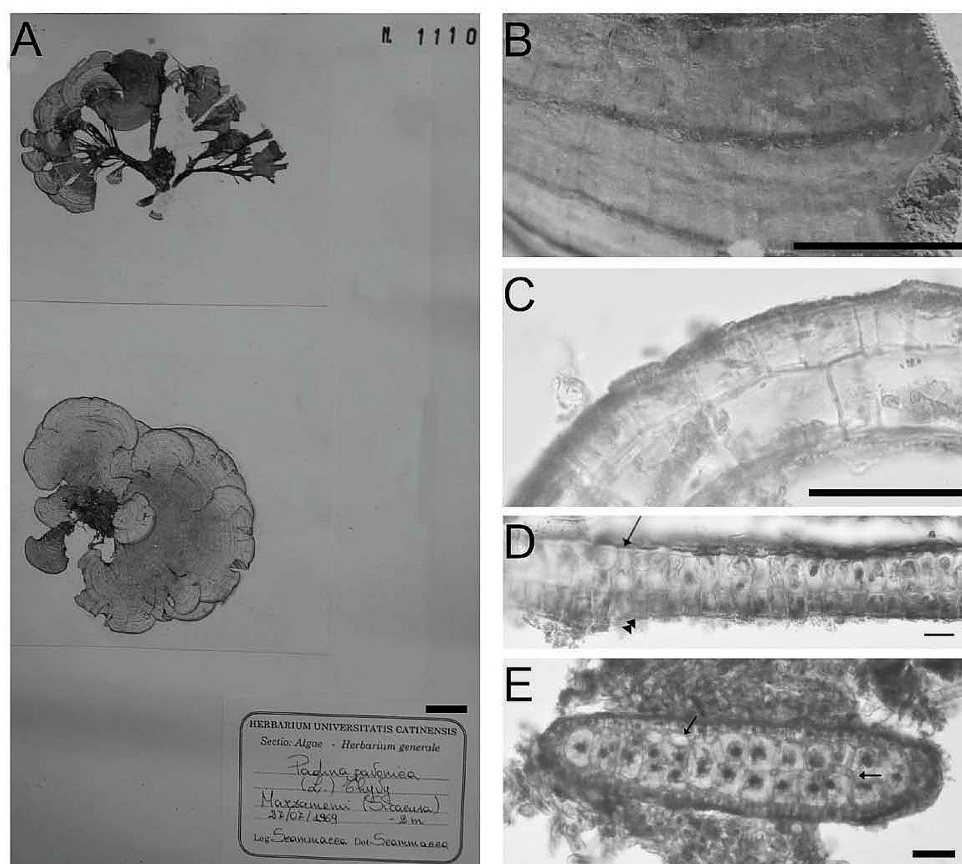


FIGURE 2. *Padina ditristromatica*. A. Herbarium sheet (CAT 1110) showing the habitus. B. Upper surface with hair lines distributed in unequal distance. C. Longitudinal section of the rolled part of the apical portion of the thallus showing 2 layers of cells. D. Cross section of the middle portion, showing a mixture of 2 (pointed by the arrows) to 3 layers (pointed by the arrowheads). E. Cross section of the basal portion of the thallus showing 2–3 layers of cells (pointed by the arrows). Photo A refers to the herbarium sheet sample. Photos B to E refer to the Santa Tecla (CT) sample. Scale bars: A, B, 1 cm; C–E, 50 µm. Photos by G. Marletta.

Finally, until now, *P. ditristromatica* has been reported in both low midlittoral and infralittoral zones up to –7m (Gómez Gómez *et al.* 2015); in this study, we observed that *P. ditristromatica* can extend to a depth of about –24m.

Padina gymnospora (Fig. 3 A–D)

Basionym:—*Zonaria gymnospora* Kützing (1859: 29)

Type locality:—VIRGIN ISLAND. St. Thomas (Herb. Sonder)

Distribution in the Mediterranean Sea:—ITALY (Sortino 1967 as *P. gymnospora sensu* Vickers)

Examined Specimens:—ITALY. Agrigento: Palma di Montechiaro, –0.5 m, 2/1/1967, CAT 1735 as *P. pavonica* cfr. *gymnospora*.

Morphology:—The *thallus* is fan-shaped (Fig. 3A), not or slightly calcified in the upper surface, and attached to the substrate with a rhizomatous holdfast. It has a smooth surface, with margins slightly undulated and a rolled apical portion. The hair lines are concentric, distributed at equal distances and are not prominent. They are present on both surfaces and are more conspicuous on the lower portion of the *thallus*. The species has 2 cell layers in the rolled apical portion (Fig. 3B), but immediately the layers become 3–4 (Fig. 3B, C) and up to 6–8 in the basal portion (Fig. 3D). In our samples, no reproductive traits were found.

Remarks:—The only report of *P. gymnospora* in Mediterranean Sea (Sortino 1967) refers to *P. gymnospora sensu* Vickers; but, this record probably should be considered as a misidentification of the tristromatic species *P. boergesenii*, as also assumed by Furnari *et al.* (2010) and Ni-Ni-Win *et al.* (2011a).

However, the herbarium specimen that we examined was collected in the same locality as the specimens reported by Sortino (1967). That specimen shows all the features of *P. gymnospora* (Kützing) Sonder (*non* Vickers) as reported by Womersley (1987) and by Allander & Kraft (1983:87) that examined the holotype of *Zonaria gymnospora* (MEL

583380 in the Sonder collection) when they described the new species *Padina boergesenii*. Therefore, this is the first supported record of *P. gymnospora* for the Mediterranean Sea.

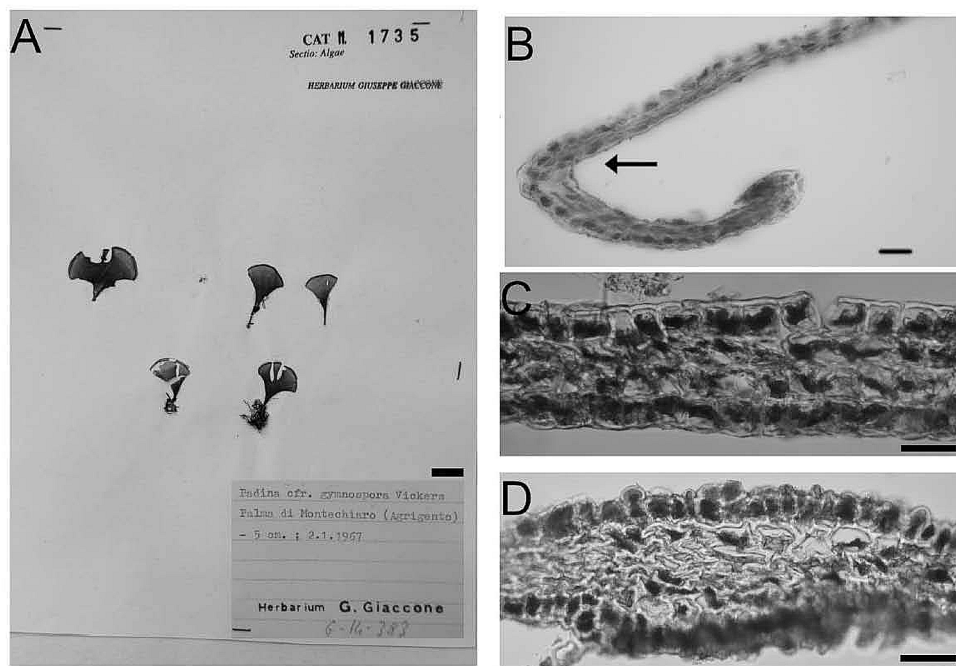


FIGURE 3. *Padina gymnospora*. A. Herbarium sheet (CAT 1735) showing the habitus. B. Longitudinal section of the rolled part of the apical portion of the thallus shows 2 cell layers in the rolled part and the transition to 3 cells (pointed by the arrow). C. Cross section of the median portion of the thallus showing 4 layers of cells. D. Cross section of the basal portion of the thallus showing 6–8 layers of cells. All photos refer to the herbarium sheet sample. Scale bars: A, 1,5 cm; B–D, 50 μ m. Photos by G. Marletta.

Padina pavonica (Fig. 4 A–G)

Basionym:—*Fucus pavonicus* Linnaeus (1753: 1162)

Type locality:—*In mari Europae australis*

Distribution in the Mediterranean Sea:—This species is widely distributed in Mediterranean ITALY, SPAIN, GREECE, FRANCE, MALTA, MOROCCO, ALGERIA, TUNISIA, LIBYA, EGYPT, ISRAEL, SYRIA, LEBANON, TURKEY (Guiry & Guiry 2023).

Examined Specimens:—ITALY. Catania: Aci Trezza, Aci Castello, –5 m, 25/04/22; ITALY. Syracuse: Penisola Magnisi, Priolo, –0,5 m, 16/06/22; ITALY. Messina: Milazzo, –0,5 m, 14/06/22; ITALY. Messina: Canne d’Organo, Filicudi Island, –0,5 m, 09/07/22; ITALY. Trapani: Cala Tramontana, Kattibuale, Scauri, Pantelleria Island, –0,5 m, 23/03/22; ITALY. Trapani: Macari, –0.5m, 06/10/2022; ITALY. Palermo: Punta Raisi, –0.5m, 07/10/2022; ITALY. Trapani: Cala Levante, Pantelleria Island, –5 m, 05/09/1970, CAT1733 and CAT1734; ITALY. Syracuse, Brucoli, Augusta, –0,5 m, 25/01/1970, CAT1104; ITALY. Palermo: Ustica, –10 m, 04/07/1967, CAT1732; ITALY. Messina: Lipari Island, –4 m, 18/05/1969, CAT1729; ITALY. Caltanissetta: Gela, –0,5 m, 29/07/1968, CAT1111; ITALY. Agrigento: Palma di Montechiaro, –1 m, 18/10/1966, CAT1722; ITALY. Messina: Capo Milazzo, –4 m, 04/04/1969, CAT1728; ITALY. Palermo: Capo Zafferano, –8m, 07/06/1969, CAT1727; ITALY. Syracuse: Ognina, –0,5 m, 12/06/1970, CAT1096.

Morphology:—The *thallus* is semicircular to circular with radial lacerations, low or not calcified on the lower surface and moderately calcified on the upper surface. It is fixed to the substrate with dense tufts of rhizoids (Fig. 4A). The hair lines are concentric, alternate between both the surfaces of the thallus and are disposed at equal distances. They are narrow-undepressed in both the surfaced. This species shows 2 cell layers in the rolled part of the apical region (Fig. 4C), 3 cell layers in the median portion (Fig. 4D) and 3–4 cell layers at the base (Fig. 4E). The medullary layers (1–2) consist of cells larger and less pigmented than the cells of the two peripheral layers (Fig. 4D). In some of our specimens (Cala Tramontana and Kattibuale in Pantelleria Island, in Filicudi Island, and Punta Raisi), the presence of the *Vaughaniella* stage was found (Fig. 4A, F). This finding agrees with the observations of Peralta (2013) and Gómez Gómez *et al.* (2015), which reported the presence of this stage in *P. pavonica*.

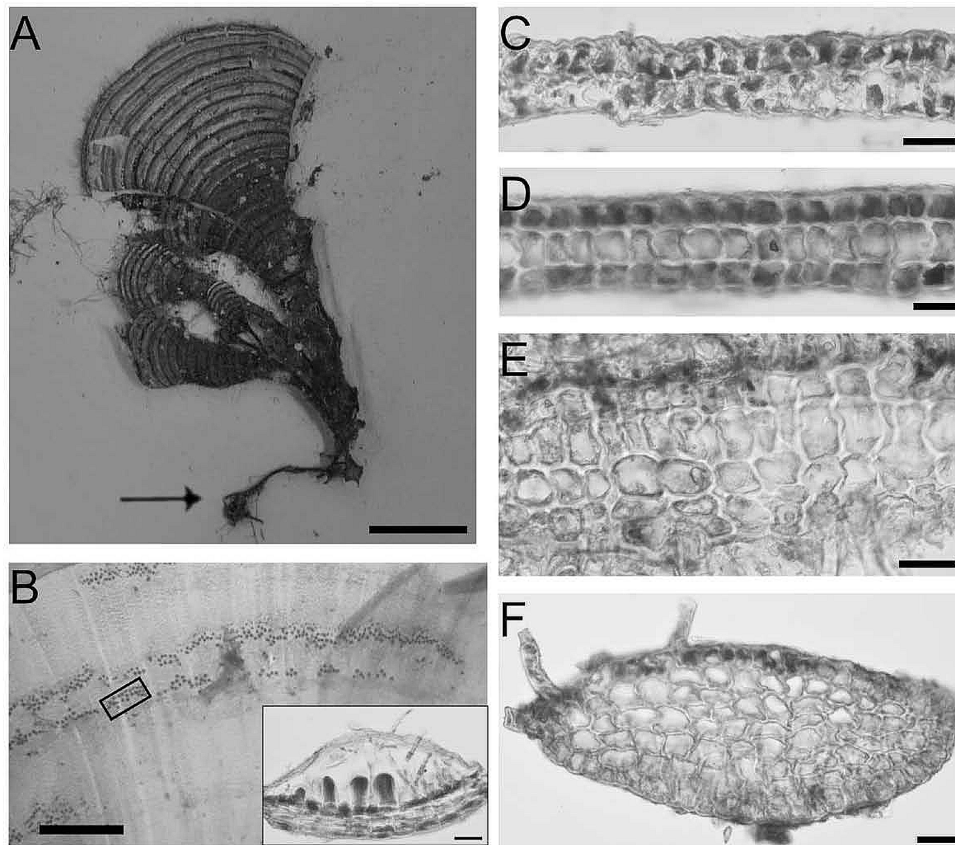


FIGURE 4. *Padina pavonica*. A. Habitus of *P. pavonica* with the *Vauganiella* stage (pointed by the arrow). B. Lower surface with broad sori above the hair lines and narrow below the hair lines; in the lower part of the picture to the right is a detail of the section of tetrasporangial sori covered with an indusium. C. Longitudinal section of the rolled part of the apical portion of the thallus showing 2 layers of cells. D. Cross section of the median portion of the thallus showing 3 layers of cells. E. Cross section of the basal portion of the thallus showing 4 layers of cells. F. Cross section of the *Vauganiella* stage. All photos refer to the sample of Pantelleria except for the photo of the sporangial sori, which refers to the herbarium sheet (CAT1734). Scale bars: A, 1 cm; B (section of tetrasporangial sori)—F, 50 μ m; B (inset), 1,5 mm. Photos by G. Marletta.

The sporangial cysts are grouped in sori, which are obovate with a basal pedicel and a transparent indusium (Fig. 4B). They are distributed only on the lower surface and form continuous lines on both sides of the hair lines, particularly they are broad above hair lines and narrow below hair lines (Fig. 4B).

Remarks:—Our observations confirm the wide distribution of the species in the Mediterranean Sea. However, as was often the case previously, the identification of this species should not be taken for granted given its similarity to other species of the genus.

Padina pavonicoides (Fig. 5 A–G)

Basionym:—*Padina pavonicoides*

Type locality:—FRANCE. Cannes: Port Cap de la Croisette.

Distribution in the Mediterranean Sea:—FRANCE (Ni-Ni-Win *et al.* 2011a). SPAIN (Ni-Ni-Win *et al.* 2011a, Gómez Gómez *et al.* 2015). TURKEY (Taskin 2013).

Examined Specimens:—ITALY. Syracuse: Brucoli, Augusta, –0,5 m, 21/05/21; ITALY. Catania: Santa Tecla, Acireale, –9,5 m, 02/07/21; ITALY. Trapani: Martingana and Scauri, Pantelleria Island, –0,5 m, 23/03/22.

Morphology:—The *thallus* is semicircular to circular with entire margin, low or not calcified on the lower surface and slightly calcified on the upper surface. It is fixed to the substrate with a short stipe, covered on the lower surface by rhizoid filaments (Fig. 5A). The hair lines are concentric, alternate between both the surfaces of the thallus and are disposed at equal distances (Fig. 5B). They are narrow-undepressed in the upper surface and broad-slightly depressed in the lower surface. This species has mainly 3 layers of cells (Fig. 5E, F), except for the rolled apical portion, which

has 2 layers of cells (Fig. 5D). In the 3-layered parts, the cells of the central layer are nearly twice as high as those of the surface layers (Fig. 5E, F). In the specimens collected at Martingana, we found the *Vaughaniella* stage (Fig. 5G).

The sporangial cysts are grouped in sori, which are obovate and with a transparent indusium (Fig. 5C) and are distributed only on the lower surface and form patches above the hair lines (Fig. 5B).

Remarks:—Until today, *P. pavonicoides* has been found only in Turkey, Spain and France. Our Sicilian records expand the distribution area of this species and show an effective continuity between the eastern and western basin. It should be noted that we collected *P. pavonicoides* also in shallow habitats, expanding the bathymetric distribution range of the species compared to what was suggested by Gómez Gómez *et al.* (2015).

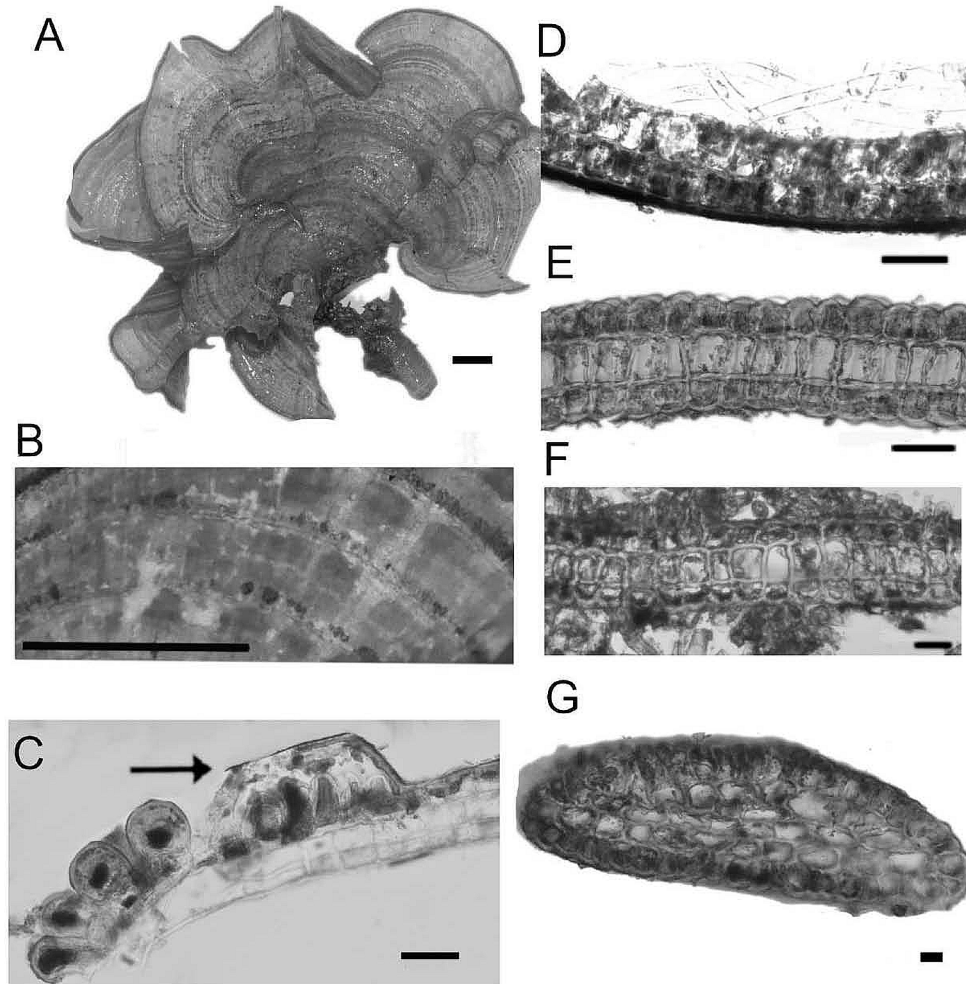


FIGURE 5. *Padina pavonicoides*. A. Habitus of *P. pavonicoides*. B. Lower surface with sporangial sori in patches above hair lines, arranged at equal distance C. Section of tetrasporangial sori covered with an indusium (pointed by the arrow). D. Longitudinal section of the rolled apical portion of the thallus showing 2 layers of cells. E. Cross section of the median portion of the thallus showing 3 layers of cells. F. Cross section of the basal portion of the thallus showing 3 layers of cells. G. Cross section of *Vaughaniella* stage. Photos A, D, and F refer to the sample of Brucoli (SR), photo G refers to the sample of Martingana—Pantelleria, and photos B, C and E refer to the sample of Scauri—Pantelleria. Scale bars: A, 1 cm; B, 0,5 cm; C–G, 50 µm. Photos by G. Marletta.

Padina tetrastromatica (Fig. 6 A–E)

Basionym:—*Padina tetrastromatica*

Type locality:—Meith (Maydh), Somalia

Distribution in the Mediterranean Sea:—SYRIA (Mayhoub 2004)

Examined Specimens:—ITALY. Palermo: Punta Raisi, –2m, 4/5/1966, CAT 1730 as *P. pavonica*.

Morphology:—The *thallus* is flabelliform (Fig. 6A) and attached to the substrate through a fibrous disc-shaped holdfast. The stipe is short, flattened, and the thallus has a light calcification on the upper surface. The species shows concentric and narrow-undepressed hair lines at an equal distance between both surfaces. The margins are smooth or slightly undulated and the upper rolled portions show a smooth surface. The thallus consists mainly of 4 layers of cells

(Fig. 6D, E), except in the rolled apical portion where only 2-cell layers are present (Fig. 6C); between the 2-cell and 4-cell portions, a short zone with 3 layers of cells can be identified.

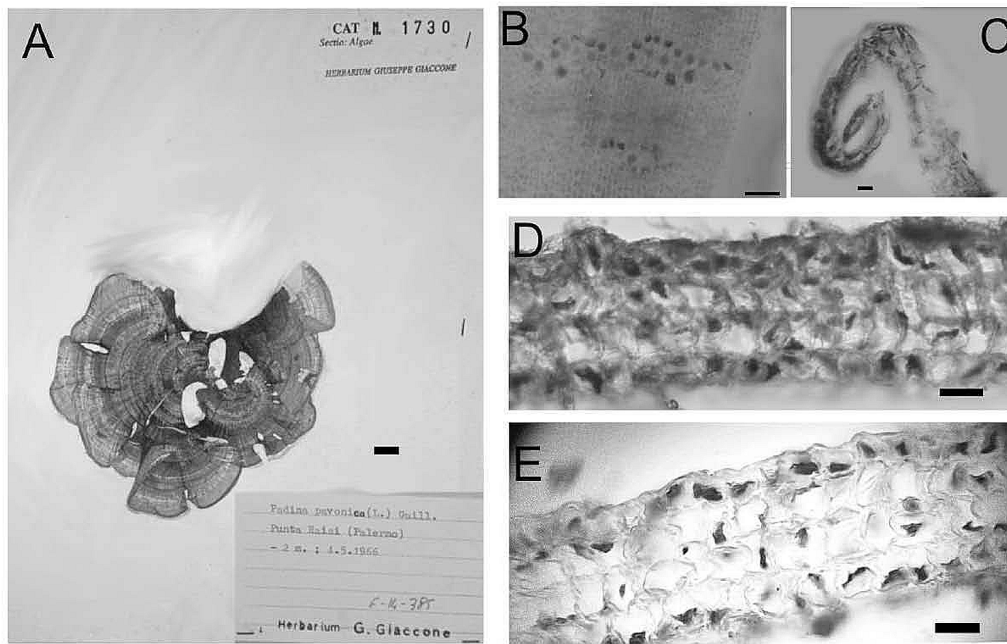


FIGURE 6. *Padina tetrastromatica*. A. Herbarium sheet (CAT 1730) showing habitus. B. Lower surface with continuous lines of sporangial sori above hair lines and discontinuous lines below the hair lines. C. Longitudinal section of the rolled part of the apical portion of the thallus. D. Cross section of the median portion of the thallus showing 4 layers of cells. E. Cross section of the basal portion of the thallus showing 4 layers of cells. All photos refer to the herbarium sheet sample. Scale bars: A, 1 cm; B, 110 µm; C–E, 50 µm. Photos by G. Marletta.

In our sample, bands of sori are present near the growth zone and are located on both sides of the hair lines, particularly they are in continuous lines above hair lines and in discontinuous lines below the hair lines (Fig. 6B). Moreover, there is no indusium and *Vauganiella* stage, the latter found instead by Aisha & Shameel (2010).

Remarks:—This Indo-Pacific species was reported in Syria in 2004 (Mayhoub 2004) but, according to Verlaque *et al.* (2015:51), its successful establishment in the Mediterranean Sea remains unknown. Our herbarium specimen attests to the presence of *P. tetrastromatica* in this basin as early as 1966. Therefore, it is very likely that this species could have a wider distribution in the Mediterranean Sea. For this reason, it is very important to accurately examine past data through the study of herbarium sheets to assess the real distribution of this species in the Mediterranean as well as a more accurate identification of new specimens of the genus *Padina* collected.

Wynne (1998) considered *P. tetrastromatica* to be a synonym of *Padina antillarum* (Kützinger) Piccone (1886: 36); but we, according to Ni-Ni-Win *et al.* (2011b), retain to maintain the two *taxa* separate until specimens from the respective type localities have been compared using sequence data.

Discussion

Until the publication of the study by Ni-Ni-Win *et al.* (2011a), in the Mediterranean Sea the genus *Padina* was considered to be represented mainly by *P. pavonica* (Gallardo *et al.* 1985, Gómez Gómez *et al.* 2015). This is probably because the old records were based on inadequate traditional morphological characters and there was no DNA sequence support data (Ni-Ni-Win *et al.* 2011a). In addition, exhaustive taxonomic studies at the species level of the genus *Padina* had not been conducted. Only after detailed molecular and morphological studies, which also detected the presence of new species of *Padina* (Ni-Ni-Win *et al.* 2011a), it was possible to redefine the distribution of species belonging to this genus in the Mediterranean Sea.

The analysis of the samples collected along the Sicilian coast, as well as the revision of the herbarium sheets, have allowed identifying five species of *Padina*: *P. ditristromatica*, *P. gymnospora*, *P. pavonica*, *P. pavonicoides*

and *P. tetrastromatica*. Particularly, some of the *herbarium* specimens, previously identified as *P. pavonica*, were misidentifications, therefore *P. ditristromatica*, *P. gymnospora*, and *P. tetrastromatica* were already present in the Mediterranean in the past.

Regarding the three-layered species, our samples of *P. pavonicoides* and *P. ditristromatica* present all the features matching the descriptions of Ni-Ni-Win *et al.* (2011a), Cormaci *et al.* (2012), Gómez Gómez *et al.* (2015). In *P. pavonicoides* there are 3-cell layers in the basal and median portions, while in *P. ditristromatica* there is a mixture of 2–3 in these portions. In both species, the sporangial sori are present only on the lower surface. The calcification is light on the upper surface and almost absent on the lower surface in *P. pavonicoides*, while it is heavy on the upper surfaces and moderate on the lower surface in *P. ditristromatica*. Moreover, although the *Vaughaniella* stage was not reported in either of these two species by Ni-Ni-Win *et al.* (2011a), we found it in our specimens of *P. pavonicoides*. Therefore, the presence of this stage can be considered as another useful diacritical character to distinguish *P. pavonicoides* from *P. ditristromatica*. Previously, Gómez Gómez *et al.* (2015) had already proposed this feature to differentiate *P. pavonica* from *P. ditristromatica*, since contrary to Ni-Ni-Win *et al.* (2011a), they had found this stage in the adults of *P. pavonica*. Also, in our specimens of *P. pavonica* we often detected the presence of this stage. In general, *P. pavonica* has features more similar to *P. pavonicoides* than to *P. ditristromatica*. *P. pavonica* differs from *P. pavonicoides* mainly in having often 4 layers of cells at the base and the sporangial sori arranged in continuous lines on both sides of the hair lines and not in patches only above hair lines, as *P. pavonicoides*.

As concerns the species with four or more cell layers, the specimens in *exsiccata* of *P. gymnospora* and of *P. tetrastromatica* (both labelled as *P. pavonica*) correspond to the descriptions of Womersley (1987) and Abbas & Shameel (2013a,b) as regards *P. gymnospora*, and Gaillard (1967), Aisha & Shameel (2010), Abbas & Shameel (2013b), Ni-Ni-Win *et al.* (2013) and Huisman (2015) as regards *P. tetrastromatica*. In *P. gymnospora* there are 3–4 cell layers in the median portion and 6–8 layers at the base. Instead, *P. tetrastromatica* shows *thalli* consisting mainly of 4 cells layered. In *P. gymnospora* the sporangial sori are generally present on both the upper and lower surfaces, while in *P. tetrastromatica* the sporangial sori are only on the lower surface. The calcification is the same in both species, light and present only on the upper surface. Moreover, in both species, the hair lines are disposed on both surfaces, but in *P. gymnospora* are more conspicuous in the lower portion of the *thallus* close to the holdfast. Our finding of *P. pavonicoides* in Sicily is the first report of this species for the Italian coast, representing a connecting line between previous reports: to the west, both in France (Ni-Ni-Win *et al.* 2011a) and Spain (Ni-Ni-Win *et al.* 2011a, Gómez Gómez *et al.* 2015) and, to the east in Turkey (Taskin 2013). This suggests that this species may have a wider distribution in the Mediterranean.

P. tetrastromatica, widely distributed in warm seas (Verlaque *et al.* 2015), was reported in the Mediterranean Sea only in Syria (Mayhoub 2004); therefore, our report expands its distribution range. In fact, it is the first report for the Italian coast but also for the whole western sector of the Mediterranean. It should also be noted that we found this species following the re-examination of *herbarium* samples and therefore, *P. tetrastromatica* was present as early as 1966 in Sicily.

P. gymnospora, was reported in the Mediterranean Sea by Ramon and Friedmann (1966) and Nizamuddin (1981) based on the predominantly tristromatic species reported by Vickers (1905) and not based on *P. gymnospora* (Kützing) Sonders, characterized instead by 2 layers of cells in the rolled apical portion, 3–4 layers of cells in the median portion and up to 6–8 layers of cells in the basal portion. Therefore, we agree with Ni-Ni-Win *et al.* (2011a) in referring to the citations made for the Mediterranean to *P. boergesenii*. In contrast, our *herbarium* specimen presents all the characteristics of *P. gymnospora* (Kützing) Sonders, therefore it is the first supported report of this species in the Mediterranean Sea.

Finally, we did not find both the presence of *P. boergesenii* and *P. boryana* in this study. However, the first species is well established along the Levantine coasts (Bitar 2017, Verlaque *et al.* 2015) including Israel (Ramon & Friedmann 1966) and Libya (Nizamuddin 1981); while reports from Malta are to be confirmed (Verlaque *et al.* 2015). Instead, the presence of *P. boryana* was only documented by Arraj *et al.* (2016) in the eastern Mediterranean.

Conclusions

In conclusion, the detailed study of the species of the genus *Padina*, which are very similar morphologically, together with the re-examination of the *herbarium* sheets, underlined the existence of misidentifications and thus it allowed to discover the existence of hitherto never reported species in Mediterranean areas. Therefore, continued and more

detailed and careful studies on this genus, could expand and redefine its distribution and biodiversity, as evidenced by the results obtained in the present work.

Key to the species of the genus *Padina* in the Mediterranean Sea.

1. Thallus with 2 layers of cells and/or a mixture of 2–3 layers of cells in the median portion2
- Thallus with at least 3 layers of cells in the median portion3
2. Thallus entirely composed of 2 layers of cells; hair lines are in concentric lines on the upper surface (ephemeral or absent in the lower surface); indusium absent..... *Padina boryana*
- Thallus with a mixture of 2–3 cell layers in the median and basal portions; hair lines alternate on both surfaces; indusium present*Padina ditristomatica*
3. Thallus with 3 layers of cells in the median portion and 3/4 in basal one; sporangial sori arranged in patches or in concentric lines; indusium present or absent4
- Thallus with more than 3 layers of cells in the median and basal portion; sporangial sori arranged in continuous or discontinuous lines; indusium always absent6
4. Thallus consisting entirely of 3 layers of cells except in the rolled apical portion; cells of the central layer and one cortical layer are more or less equal in height and usually smaller than the other cortical layer; sporangial sori arranged in concentric lines separated from each other by a sterile zone delimited by two consecutive hair lines on alternate surfaces of frond; indusium absent.....
-*Padina boergesenii*
- Thallus with 3 layers of cells in the median portion and 3/4 in basal ones; medullary layers (central layers) (1–2) consist of cells larger and less pigmented than the cells of the two peripheral layers; indusium present.....5
5. Thallus with 3 layers of cells in the median portion and 3/4 in basal ones; sporangial sori arranged in continuous lines on both sides of the hair lines *Padina pavonica*
- Thallus with 3 layers of cells in both the median and basal portions; sporangial sori arranged in patches above hair line; indusium present.....*Padina pavonicoides*
6. Thallus with 3–4 layers of cells in the median portion and 4 layers in the basal portion; sporangial sori present only on the lower surface arranged in continuous lines above the hair lines and discontinuous lines below the hair lines *Padina tetrastomatica*
- Thallus with 3–4 layers of cells in the median portion and 6–8 layers of cells in the basal portion; sporangial sori present in both surfaces of the thallus arranged in more or less continuous lines*Padina gymnospora*

Acknowledgements

This work was supported by grants from the University of Catania through Piano di incentivi per la ricerca di Ateneo 2020/2022 (Pia.ce.ri.)—Ricerca Dipartimentale as well as Fondi di Ateneo 2020–2022—linea open access. We also would like to thank Dr. A. I. Di Paola for collecting the samples from Filicudi, Aeolian Islands.

References

- Abbas, A. & Shameel, M. (2013a) Occurrence of *Padina gymnospora* (Phaeophycota) at the coast of Karachi. *Pakistan Journal of Botany* 45: 341–344.
- Abbas, A. & Shameel, M. (2013b) Morpho-anatomical studies on the genus *Padina* (Dictyotales, Phaeophycota) from the Coast of Karachi, Pakistan. *Proceedings of the Pakistan Academy of Sciences* 50: 21–36.
- Adanson, M. (1763) *Familles des plantes*. II. Partie [Vol. 2]. Paris: Chez Vincent, Imprimeur-Librairie de Mgr le Comte de Provence, rue S. Servin. pp. [1–24], [i–iii], [1]–640.
<https://doi.org/10.5962/bhl.title.271>
- Aisha, K. & Shameel, M. (2010) Occurrence of the genus *Padina* (Dictyophyceae, Phaeophycota) in the coastal waters of Karachi. *Pakistan Journal of Botany* 42: 319–340.
- Allander, B.A. & Kraft, G.T. (1983) The marine algae of Lord Howe Island (NSW): the Dictyotales and Cutleriales (Phaeophyta). *Brunonia* 6: 73–130.
<https://doi.org/10.1071/BRU9830073>
- Arraj, H., Mayhoob, H. & Abbas, A. (2016) First records of two *Padina* species (Dictyotales, Phaeophyceae) from the Syrian coast (eastern Mediterranean). *Marine Biodiversity Records* 9: 1–5.
<https://doi.org/10.1186/s41200-016-0090-x>
- Barceló, M.C., Gómez Garreta, A., Ribera, M.A. & Rull Lluch, J. (1998) Mapas de distribución de algas marinas de la Península Ibérica e Islas Baleares. XI. *Lobophora variegata* (Lamour.) Womersley, *Padina pavonica* (L.) Thivy y *Zonaria tournefortii* (Lamour.) Mont. (Dictyotales, Fucophyceae). *Botanica Complutensis* 22: 179–186.

- Børgesen, F. (1951) Some marine algae from Mauritius. Additions to the parts previously published III. *Biologiske meddelelser Kongelige danske videnskabernes selskab, Copenhagen* 18 (16): 1–44.
- Bory de Saint-Vincent, J.B.G.M. (1827) Padine. *Padina*. In: *Dictionnaire Classique d'Histoire Naturelle*. (Audouin, I. et al. Eds) Vol. 12. Paris: Rey et Gravier; Baudouin Frères, pp. 589–591.
- Bottalico, A., Alongi, G. & Perrone, C. (2016) Macroalgal diversity of Santa Cesarea-Castro (Salento Peninsula, southeastern Italy). *Anales del Jardín Botánico de Madrid* 73: 1–12.
<https://doi.org/10.3989/ajbm.2412>
- Catra, M. & Alongi, G. (2013) On some new and interesting marine macroalgae from the Greek coasts (Mediterranean Sea). *Nova Hedwigia* 97: 503–514.
<https://doi.org/10.1127/0029-5035/2013/0124>
- Cecere, E., Cormaci, M., Furnari, G., Petrocelli, A., Saracino, O. & Serio, D. (1996) Benthic algal flora of Cheradi Islands (Gulf of Taranto, Mediterranean Sea). *Nova Hedwigia* 62: 191–214.
- Cormaci, M., Furnari, G., Catra, M., Alongi, G. & Giaccone, G. (2012) Flora marina bentonica del Mediterraneo: Phaeophyceae. *Bollettino Dell'Accademia Gioenia* 45: 1–508.
- Cribb, A.B. (1951) Invalidation of the genus *Vaughaniella*. *Nature* 168: 302.
<https://doi.org/10.1038/168302a0>
- De Clerck, O. & Coppejans, E. (1997) Notes on the *Dictyota vieillardii* and *D. adnata* (Dictyotaceae, Phaeophyta). *Taxon* 46: 33–36.
<https://doi.org/10.2307/1224289>
- Furnari, G., Cormaci, M. & Serio, D. (1999) Catalogue of the benthic marine macroalgae of the Italian coast of the Adriatic Sea. *Bocconeia* 12: 1–214.
- Furnari, G., Giaccone, G., Cormaci, M., Alongi, G., Catra, M., Nisi, A. & Serio, D. (2010) Macrophytobenthos. In: Relini, G. (Ed.) Checklist of the flora and fauna in Italian seas (Parte II). *Biologia Marina Mediterranea* 17: 801–828.
- Gaillard, J. (1967) Étude monographique de *Padina tetrastromatica* (Hauck). *Bulletin de l'Institut Fondamental d'Afrique Noire, Série A, Sciences Naturelles* 29: 447–463.
- Gallardo, T., Gómez Garreta, A., Ribera, M.A., Álvarez, M. & Conde, F. (1985) *A preliminary checklist of Iberian benthic marine algae*. Real Jardín Botánico Madrid 83 pp.
- Gómez Gómez, A., Poch, B.P., Ribas, F.R., Garreta, A.G., Siguan, M.A.R. & Lluch, J.R. (2015) *Padina ditristromatica* and *Padina pavonicoides* (Dictyotales, Phaeophyceae): two new records for the marine benthic flora of the Mediterranean Spanish coasts. *Cryptogamie Algologie* 36: 55–63.
<https://doi.org/10.7872/crya.v36.iss1.2015.55>
- Gómez-Garreta, A., Rull-Lluch, J., Barceló Martí, M.C. & Ribera Siguan, M.A. (2007) On the presence of fertile gametophytes of *Padina pavonica* (Dictyotales, Phaeophyceae) from the Iberian coasts. *Anales del Jardín Botánico de Madrid* 64: 27–33.
<https://doi.org/10.3989/ajbm.2007.v64.i1.48>
- Guiry, M.D. & Guiry, G.M. (2023) AlgaeBase, National University of Ireland, Galway. Available from: <http://www.algaebase.org> (accessed: 14 April 2023)
- Hauck, F. (1887) Ueber einige von J.M. Hildebrandt im Rothen Meere und Indischen Ocean gesammelte Algen III, IV. *Hedwigia* 26: 18–21, 41–45.
- Huisman, J. (2015) *Algae of Australia: marine benthic algae of north-western Australia. Volume 1*. Csiro publishing. 320 pp.
- Kützinger, F.T. (1859) *Tabulae phycologicae; oder, Abbildungen der Tange*. Vol. IX [9]. Nordhausen: Gedruckt auf kosten des Verfassers, pp. i–vii, 1–42, 100 pls.
- Linnaeus, C. (1753) *Species plantarum*, exhibentes plantas rite cognitatas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. Vol. 2. Holmiae [Stockholm]: Impensis Laurentii Salvii, pp. [i], 561–1200, [1–30, index], [i, err.].
<https://doi.org/10.5962/bhl.title.669>
- Ni-Ni-Win, Hanyuda, T., Draisma, S.G.A., Furnari, G., Meinesz, A. & Kawai, H. (2011a) *Padina ditristromatica* sp. nov. and *Padina pavonicoides* sp. nov. (Dictyotales, Phaeophyceae), two new species from the Mediterranean Sea based on morphological and molecular markers. *European journal of phycology* 46 (4): 327–341.
<https://doi.org/10.1080/09670262.2011.614355>
- Ni-Ni-Win, Hanyuda, T., Arai, S., Uchimura, M., Prathep, A., Draisma, S.G.A., Phang, S.M., Abbott, I.A., Millar, A.J.K. & Kawai, H. (2011b) A taxonomic study of the genus *padina* (dictyotales, phaeophyceae) including the descriptions of four new species from japan, hawaii, and the andaman sea. *Journal of Phycology* 47 (5): 1193–1209.
<https://doi.org/10.1111/j.1529-8817.2011.01054.x>
- Ni-Ni-Win, Hanyuda, T., Draisma, S.G., Lim, P.E., Phang, S.M. & Kawai, H. (2013) *Taxonomy of the genus Padina (Dictyotales, Phaeophyceae) based on morphological and molecular evidences, with key to species identification*. Taxonomy of Southeast Asian

Seaweeds II, University of Malaya Press, 119 pp.

- Nizamuddin, M. (1981) Contribution to the marine algae of Libya Dictyotales. *Bibliotheca Phycologica* 54: 1—map.
- Mayhoub, H. (2004) The presence of tropical alga *Padina tetrastromatica* Hauck near Latakia (Syria). *Damascus University Journal* 2: 77–89.
- Peralta, P.B. (2013) *Morfogénesis y fenología de dos especies de Padina del litoral catalán: P. ditristomatica y P. pavonica*. Màster de Ciències del Mar: Oceanografia i Gestió del Medi Marí. Universitat de Barcelona. 31 pp.
- Piccone, A. (1886) *Alghe del viaggio di circumnavigazione della Vettor Pisani*. Genova [Genoa]: Tipografia del Reale Istituto Sordo-Muti, pp. [1]–97, 2 pls.
<https://doi.org/10.5962/bhl.title.64275>
- Ramon, E.D.I.T.H. & Friedmann, I. (1966) *The gametophyte of Padina in the Mediterranean*. In: *Proceedings of the Fifth International Seaweed Symposium Halifax, August 25–28, 1965*. Pergamon, pp. 183–196.
<https://doi.org/10.1016/B978-0-08-011841-3.50031-8>
- Ribera, M.A., Gómez Garreta, A., Gallardo, T., Cormaci, M., Furnari, G. & Giaccone, G. (1992) Check-list of Mediterranean Seaweeds. I. Fucophyceae (Warming 1884). *Botanica Marina* 35: 109–130.
<https://doi.org/10.1515/botm.1992.35.2.109>
- Rindi, F., Sartoni, G. & Cinelli, F. (2002) A floristic account of the benthic marine algae of Tuscany (Western Mediterranean Sea). *Nova Hedwigia* 74: 201–250.
<https://doi.org/10.1127/0029-5035/2002/0074-0201>
- Serio, D., Alongi, G., Catra, M., Cormaci, M. & Furnari, G. (2006) Changes in the benthic algal flora of Linosa Island (Straits of Sicily, Mediterranean Sea). *Botanica Marina* 49: 135–144.
<https://doi.org/10.1515/BOT.2006.018>
- Silberfeld, T., Bittner, L., Fernández-García, C., Cruaud, C., Rousseau, F., De Reviers, B., Leliaert, F., Payri, C.E. & De Clerck, O. (2013) Species diversity, phylogeny and large scale biogeographic patterns of the genus *Padina* (Phaeophyceae, Dictyotales). *Journal of phycology* 49 (1): 130–142.
<https://doi.org/10.1111/jpy.12027>
- Sonder, O.G. (1871) Die Algen des tropischen Australiens. *Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben von dem Naturwissenschaftlichen Verein in Hamburg* 5 (2): 33–74
- Sortino, M. (1967) Flora e vegetazione terrestre e marina del litorale di Palma di Montechiaro (AG). *Lavori dell'Istituto Botanico Giardino Coloniale di Palermo* 23: 1–112.
- Taskin, E. (2013) New records of three dictyotalean brown algae for Turkey. *Botanica Marina* 56: 299–302.
<https://doi.org/10.1515/bot-2013-0012>
- Taylor, W.R. (1960) *Marine algae of the eastern tropical and subtropical coasts of the Americas*. Ann Arbor: The University of Michigan Press, pp. [i]–xi, 1–870, 14 figs, 80 pls.
- Taylor, W.R. (1966) Records of Asian and western Pacific marine algae, particularly algae from Indonesia and the Philippines. *Pacific Science* 20: 342–359
- Tsekos, I. & Haritonidis, S. (1977) A survey of the marine algae of the Ionian Islands, Greece. *Botanica Marina* 20: 47–65.
<https://doi.org/10.1515/botm.1977.20.1.47>
- Tsiamis, K., Panayotidis, P., Economou-Amilli, A. & Katsaros, C. (2013) Seaweeds of the Greek coasts. I. Phaeophyceae. *Mediterranean Marine Science* 14: 141–157.
<https://doi.org/10.12681/mms.315>
- Umezaki, I. & Yoneda, Y. (1962) Morphological and embryonal studies of *Padina japonica* Yamada. *Acta Phytotaxonomica et Geobotanica* 19: 80–91.
<https://doi.org/10.18942/bunruichiri.KJ00001077888>
- Verlaque, M., Ruitton, S., Mineur, F. & Boudouresque, C.F. (2015) *CIESM atlas of exotic species in the Mediterranean: 4. Macrophytes*. CIESM Publications, Monaco, 364 pp.
- Vieira, C., Steen, F., D'hondt, S., Bafort, Q., Tyberghein, L., Fernandez-García, C., Wysor, B., Tronholm, A., Mattio, L., Payri, C., Kawai, H., Saunders, G., Leliaert, F., Verbruggen, H. & De Clerck, O. (2021) Global biogeography and diversification of a group of brown seaweeds (Phaeophyceae) driven by clade-specific evolutionary processes. *Journal of Biogeography* 48 (4): 703–715.
<https://doi.org/10.1111/jbi.14047>
- Womersley, H.B.S. (1987) *The marine benthic flora of southern Australia. Part II*. South Australian Government Printing Division, Adelaide, 484 pp.
- Wynne, M.J. (1998) A study of *Padina antillarum* (Kützinger Piccone and a comparison with *P. tetrastromatica* Hauck (Dictyotales, Phaeophyta). *Cryptogamie Algologie* 4: 271–289.