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Diversity and distribution of *Udotea* genus J.V. Lamouroux (Chlorophyta, Udoteaceae) in the Yucatan peninsula littoral, Mexico

JULIO ADULFO ACOSTA-CALDERÓN[1], CÉSAR HERNÁNDEZ-RODRÍGUEZ[2], ÁNGELA CATALINA MENDOZA-GONZÁLEZ[1] & LUZ ELENA MATEO-CID[1*]

[1]*Instituto Politécnico Nacional, Escuela Nacional de Ciencias Biológicas, Departamento de Botánica. Campus Santo Tomas. Carpio y Plan de Ayala, C.P. 11340. Ciudad de México.*

[2]*Instituto Politécnico Nacional, Escuela Nacional de Ciencias Biológicas, Departamento de Microbiología. Campus Santo Tomas. Carpio y Plan de Ayala, C.P. 11340. Ciudad de México*

Corresponding author: [1,]luzmcyd@gmail.com*

Abstract

A survey of the diversity, distribution, and taxonomy of the genus *Udotea* from the Yucatan peninsula littoral, Mexico, is presented. The results are based on a review of herbarium specimens, bibliographic data, and collections made by the authors during 2012–2016 at 34 localities along the study area. Macro and microscopic characteristics, relevant photographs, and descriptions are provided for each taxon. A total of 17 taxa of *Udotea* were recognized. One new record is cited for Quintana Roo, two for Yucatan, and five for Campeche coasts. The Quintana Roo littoral presents the highest number of *Udotea* species (17), followed by Campeche (13), and finally Yucatan (9). The *Udotea* taxa could be segregate by the presence of lateral appendages in the blade siphons and, the shape of the lateral appendages of the blade and stipe siphons.

Key words: Bryopsidales, Campeche, macroalgae, new records, taxonomy, Quintana Roo

Introduction

The genus *Udotea* J. V. Lamouroux (1812) is characterized by a green macroscopic coenocytic erect thalli composed of three parts: 1) an uncalcified, basal, rhizoidal mass anchored to rock or soft substrata such a sand, mud, or peat; 2) an upright calcified and corticated stalk (= stipe); and 3) a calcified funnel or fan shaped terminal blade (= flabellum). Each stalk consists of central longitudinal siphons surrounded by lateral appendages that form a distinct cortical layer. The blade is composed of dichotomously branched siphons (uncorticated blade) that, in some cases, bear simple to variously compound lateral appendages (corticated blade) (Littler & Littler 1990). The species of *Udotea* have an anchoring system composed of a net of rhizoids that binds sediments to form holdfast in unconsolidated sediments and function as early colonizers facilitating later establishment of the seagrasses (Zieman *et al.* 1989, Williams 1990, Collado-Vides *et al*. 1998, Bedinger *et al*. 2013). Also, they are well-recognized as calcareous sediment producers because, even after death, the heavily calcified thalli of the Udoteaceae contribute to sand production, reef building, and provide organic matter that improves sediment nutrients when thalli decompose (Williams 1990, Hillis-Collinvaux 1997, Harney & Fletcher 2003, Van Tussenbroek & Van Dijk 2007). Besides being important primary producers, shelter and nursery grounds, they are food sources for several marine organisms (Hay 1997, Hay & Fenical 1998). Worldwide, 41 infrageneric taxa of *Udotea* genus have been described with strictly marine specimens in tropical waters (Guiry & Guiry 2017). Littler & Littler (1990) cited 21 taxa of *Udotea* for the Tropical Western Atlantic. Recently, Wynne (2017) recorded 23 infrageneric taxa (17 species, five forms and one variety) for the tropical and subtropical Western Atlantic, of them 16 have been documented for the littoral of the Yucatan peninsula: Sixteen taxa of *Udotea* have been reported for Quintana Roo coast (Huerta-Múzquiz 1958, Huerta-Múzquiz & Garza-Barrientos 1966, Taylor 1972, Garza-Barrientos 1975, Huerta-Múzquiz & Garza-Barrientos 1980, Huerta-Múzquiz *et al*. 1987, Aguilar-Rosas *et al*. 1989, Aguilar-Rosas 1990, Mendoza-González & Mateo-Cid 1992, Dreckmann *et al*. 1996, Aguilar-Rosas *et al*. 1998, Mendoza-González *et al*. 2000, Aguilar-Rosas *et al.* 2001, Mateo-Cid & Mendoza-González 2007, Collado-

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Vides *et al*. 2009, Acosta-Calderón *et al*. 2016); whereas eight species have been cited for the coast of Campeche (Huerta-Múzquiz & Garza-Barrientos 1966, Huerta-Múzquiz *et al*. 1987, Callejas-Jiménez *et al*. 2005, Mateo-Cid *et al*. 2013, Mendoza-González *et al.* 2016); finally, only four species of *Udotea* have been recorded in the insular and littoral region of Yucatan (Huerta-Múzquiz *et al*. 1987, Ortegón-Aznar *et al.* 2001, Sánchez-Molina *et al.* 2007, Rosado-Espinoza *et al*. 2012, Ortegón-Aznar & Aguilar-Perera 2014). Despite their ecological importance in tropical marine ecosystems, surprisingly little is known about the occurrence of this genus at the Yucatan peninsula littoral because many coastal areas remain unexplored, specifically in Campeche and Yucatan, and there are no descriptions of the morphology and anatomy of *Udotea* from the Yucatan peninsula coast. The aim of this study is to provide an updated revision of the diversity and distribution of the *Udotea* genus from the coast of the Yucatan peninsula and, thus, establish the bases for future taxonomic, ecological, and biogeographical studies.

Material and methods

Study area

The Yucatan peninsula is a biogeographical area located in the Southeast of the Mexican Republic and comprises the states of Campeche and Yucatan at the Gulf of Mexico, and Quintana Roo at the Caribbean Sea (Fig. 1). The Yucatan peninsula has 1940 km of shoreline with a wide variety of ecosystems ranging from mangroves, sandy and rocky beaches, seagrass meadows, and coral reefs, resulting in a heterogeneous landscape. The region of the Gulf of Mexico is a wide continental shelf of over 260 km, whereas the Caribbean shelf is very narrow, less than 20 km, with a barrier and lagoon reef that offers more variety of habitats (Britton & Norton 1989, Wilkinson *et al.* 2009). The North and West coasts of the peninsula (Campeche-Yucatan) have sandy bottom beaches and coastal lagoons with mangroves. The East coast of the peninsula, which corresponds to Quintana Roo, has areas of coast with rocky substrate, although still dominated by a sandy bottom including its large bays and lagoons (De la Lanza-Espino 1991, Fernández-Equiarte *et al.* 1993). The Yucatan peninsula littoral is characterized by marine currents and groundwater discharges (Herrera-Silveira & Morales-Ojeda 2010). The study area is influenced by three well-defined seasons: dry (March to May), rainy (June to October), and "nortes" (November to February), which is dominated by cold fronts. Additionally, a tropical cyclone activity season (from June to November) has a strong influence on coastal environmental stability (Mendoza-González *et al*. 2016).

Field and laboratory work

Considering the references, accessibility, and environmental heterogeneity, 34 sampling locations were established along the littoral of the Yucatan peninsula (Table 1). Collections were made by snorkeling in subtidal zones; while specimens in the intertidal zone were collected during low tide periods by hand picking in different habitats, like rocky and sandy bottoms. Collections were made during June, September, December 2014; April, October 2015; January, June 2016 (Fig. 1). Algae were preserved in 5% formalin-seawater. Small segments of the stipe and blade were decalcified with 0.6 N HNO_3 and stained with cresil blue for anatomical observations and measurements. Semi-permanent slides were prepared using corn syrup/water (1:1) with a trace of phenol added to prevent fungal growth. Species were identified following Littler & Littler (1990). Photomicrographs were taken with a Sony MPEGMOVIEVX (Tokyo, Japan) coupled to an Olympus CX31 Microscope (Manila, Philippines), and digital images were edited and assembled on plates using Gimp 2.8 (free version). Specimens are housed at the ENCB herbarium (Department of Botany, National School at Biological Sciences, Mexico City). Additionally, specimens of *Udotea* were borrowed from the ENCB herbarium for further analyses. An update list of taxa of *Udotea* genus from the Yucatan peninsula littoral was made based on literature, herbarium data and collections. The taxonomic status of the species was verified with Guiry & Guiry (2017). According to the collection and herbarium data, distribution maps of the taxa were elaborated using ArcView Software. Description of the morphology, anatomy, reproductive characters, and information related to the habitat, the geographic distribution, and the examined specimens are included for each taxon. Descriptive terminology follows Littler & Littler (1990).

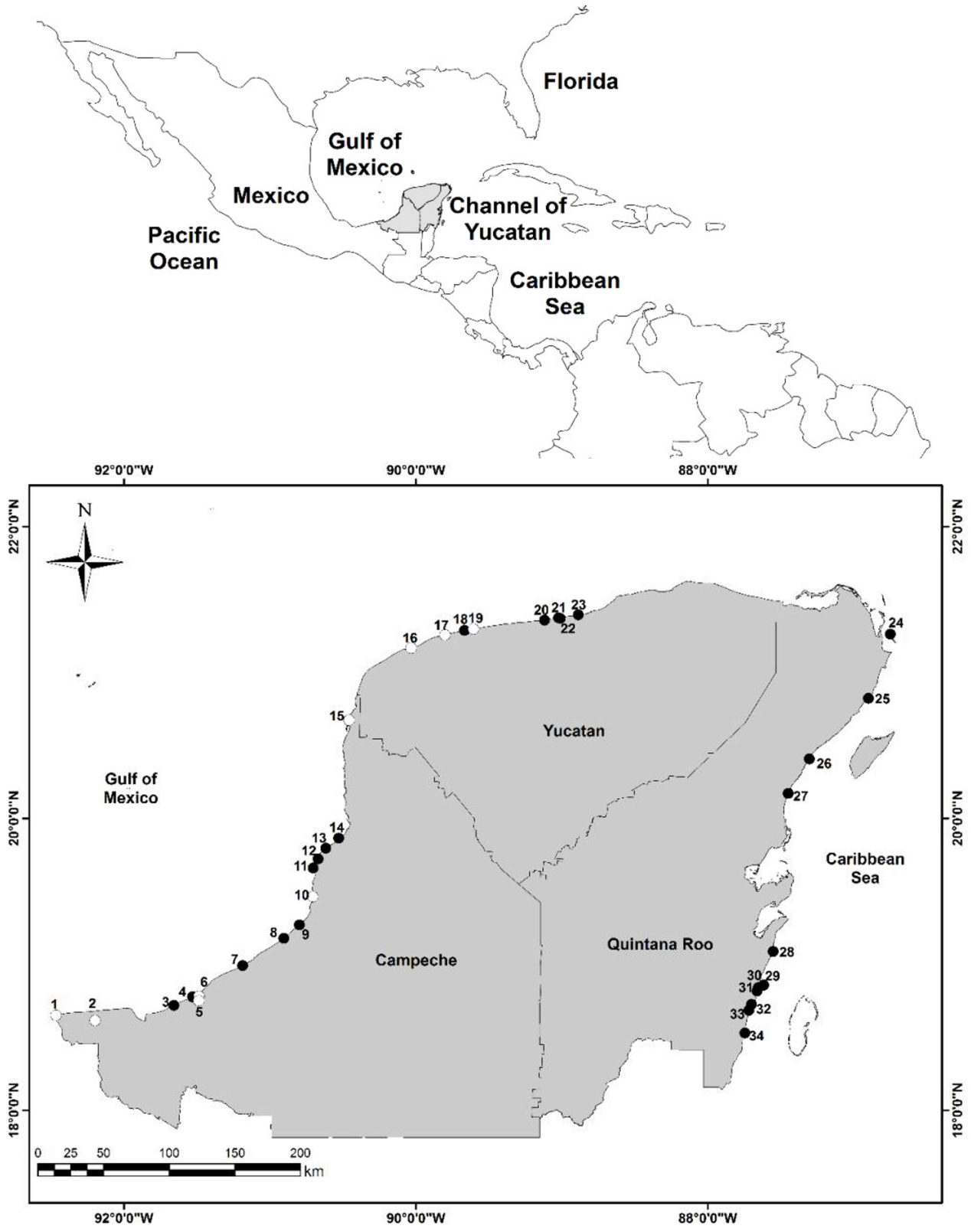


FIGURE 1. Study area and distribution of *Udotea* genus in the Yucatan peninsula littoral.

TABLE 1. Geographical coordinates of sampling locations in the Yucatan peninsula, Mexico.

#	Localities	LATITUDE N	LONGITUDE W
	CAMPECHE		
1	Nuevo Campechito	18° 39′04′′	92° 27′58′′
2	Laguna Pom	18° 36′56′′	92° 11′55′′
3	Ensenada	18° 43′09′′	91° 39′28′′
4	Puerto Real	18° 46′40′′	91° 31′48′′
5	Isla Aguada	18° 46′54′′	91° 29′12′′
6	Isla Tortuga	18° 45′10′′	91° 29′18′′
7	Sabancuy	18° 59′32′′	91° 11′15′′
8	Punta Xen	19° 10′46′′	90° 54′19′′
9	Playa Villamar	19° 16′13′′	90° 47′54′′
10	Puente Ichao	19° 27′48′′	90° 42′25′′
11	Payucán	19° 39′37′′	90° 42′15′′
12	Xpicob	19° 43′21′′	90° 40′10′′
13	Lerma	19° 47′46′′	90° 37′01′′
14	Campeche	19° 51′55′′	90° 31′43′′
15	Isla Arena	20° 40′22′′	90° 27′28′′
	YUCATAN		
16	Sisal	21°10′02′′	90° 01′58′′
17	Chuburná	21°15′25′′	89° 48′02′′
18	Progreso	21°17′35′′	89°39′25′′
19	Chicxulub	21°17′48′′	89° 36′20′′
20	Chabihau	21°21′27′′	89° 07′05′′
21	Santa Clara Puente	21°21′52′′	89°04′55′′
22	Santa Clara Pueblo	21°22′28′′	89° 01′20′′
23	Dzilam de Bravo	21°23′40′′	88° 53′14′′
	QUINTANA ROO		
24	Isla Mujeres	21°15′42′′	86°44′50′′
25	Puerto Morelos	20°49′23′′	86° 53′53′′
26	Punta Akumal	20°24′27′′	87° 18′12′′
27	Punta Piedra	20°10′16′′	87° 26′53′′
28	Pulticub	19°05′17′′	87° 33′03′′
29	Uvero	18°51′28′′	87° 36′58′′
30	Punta Placer	18°50′25′′	87°39′10′′
31	Rio Indio	18°49′02′′	87° 39′46′′
32	Punta Mahahual	18°43′35′′	87° 42′02′′
33	Punta Rio Bermejo	18°41′09′′	87° 43′06′′
34	Santa Rosa	18°31′47′′	87° 44′42′′

DNA isolation and nucleotide sequencing

Partial sequence of the *rbc*L gene sequences was used to verify the identity of the genus *Udotea* from the collected samples. A total of ten field collected samples of *Udotea* algae (six corticated and four uncorticated specimens) were preserved in silica gel desiccant (Merck, Darmstadt, Germany) before DNA extraction. The DNA was extracted following Dellaporta *et al*. (1983) protocol. The primers pairs designed and used were 5′GCTTATGCWAAAACATTYCAAGC′3 (forward); 5′AATTTCTTTCCAAACTTCACAAGC′3 (reverse). Amplification reaction of 25 µL were performed using 2.5 µL Buffer 10X (Invitrogen ™), 2 mM $MgCl_2$, 0.24 mM dNTPs, 5 µM of each primer, 0.6 µL BSA (Thermo Scientific™), 1.75 units Taq Polymerase (Invitrogen™) and 2.0 µL of template DNA (50 and 100 ng). Cycling profile (Applied Biosystems Termocycler) consisted of 3 min at 92°C (denaturation); then 35 cycles of: denaturation 35 s at 94°C, annealing 1 min at 50°C and extension 1 min at 72°C; and final extension 10 min at 72°C. Products were checked for length using 1% agarose TBE gel with 1 µg mL^{-1} ethidium bromide and a 1000 kb ladder (Invitrogen). PCR products were cleaned using PCR Purification kit (Jena Bioscience, Jena, Germany) and sequenced in both directions with the PCR primers by Macrogen (Macrogen Inc., Seoul, Korea) using the BigDye TM terminator method. Sequences were aligned with the MUSCLE algorithm of SeaView software (Gouy *et al*. 2010). A total of five *rbc*L sequences of *Udotea*, *Penicillus* and, *Rhipocephalus* were obtained from GenBank database (Lam & Zechman 2006, Verbruggen *et al*. 2009) and added to our sequences alignments. A sequence of *Acetabularia crenulata* was used as outgroup for the analysis (Table 2). A Maximum Likelihood analysis was carried out using MEGA5 software (Tamura *et al*. 2011) with a Jukes-Cantor model and, 1000 bootstraps replicates (Felsenstein 1985) to branch support.

TABLE 2. Taxon sampling for phylogenetic analysis.

Taxon	Collection location	Source of data	Accession
Penicillus capitatus	St. Ann Parish, Priory, Jamaica	Verbruggen *et al*. (2009)	FJ432641
Rhipocephalus phoenix f. *brevifolius*	Florida Keys, USA	Lam & Zechman (2006)	AY942172
Udotea conglutinata	Bancho Chinchorro, Quintana Roo, Mexico	Lam & Zechman (2006)	AY942168
Udotea cyathiformis var. *flabellifolia*	Villamar, Campeche, Mexico	In this study	MG873194
Udotea flabellum	Banco Chinchorro, Quintana Roo, Mexico	Lam & Zechman (2006)	AY942166
Udotea flabellum	Lerma, Campeche, Mexico	In this study	MG873193
Udotea flabellum	Ensenada, Campeche, Mexico	In this study	MG873196
Udotea flabellum	Payucán, Campeche, Mexico	In this study	MG873192
Udotea flabellum	Punta Akumal, Quintana Roo, Mexico	In this study	MG873190
Udotea flabellum	Punta Herradura, Quintana roo, Mexico	In this study	MG873189
Udotea looensis	Progreso, Yucatan, Mexico	In this study	MG873188
Udotea looensis	Villamar, Campeche, Mexico	In this study	MG873191
Udotea dixonii	Payucan, Campeche, Mexico	In this study	MG873195
Udotea spinulosa	Florida Keys, USA	Lam & Zechman (2006)	AY942160
Udotea luna	Progreso, Yucatan, Mexico	In this study	MG873197
Outgroup			
Acetabularia crenulata	Bermuda	Zechman (2003)	AY177737

Results

Diversity

The collections at 34 sampling locations and the review of literature and herbarium data led to the recognition of 17 infrageneric taxa of *Udotea* in the Yucatan peninsula littoral. Total of 16 taxa have been previously cited in the literature, which 14 were confirmed by the samplings. *Udotea unistratea* D.S. Littler & M.M. Littler and *Udotea occidentalis* A. Gepp & E. Gepp were not found in the sample locations. Moreover, *Udotea norrisii* D.S. Littler & M.M. Littler is reported for first time at Yucatan peninsula. *Udotea verticillosa* A. Gepp & E. Gepp record from Quintana Roo littoral was misidentified and was re-identified as *Udotea caribaea*. Additionally, *Udotea abbottiorum* D.S. Littler & M.M. Littler, *Udotea cyathiformis* var. *flabellifolia* D.S. Littler & M.M. Littler, and *Udotea luna* D.S. Littler & M.M Littler are cited for first time to the Campeche coast. Furthermore, *Udotea cyathiformis* Decaisne, *Udotea dotyi* D.S. Littler & M.M. Littler, and *Udotea looensis* D.S. Littler & M.M. Littler are cited for first time for the Yucatan coast (Table 3). The data shows that the Quintana Roo coast presents the highest number of *Udotea* taxa with 17, followed by Campeche with 13, and Yucatan with 9.

TABLE 3. Updated list of *Udotea* taxa from the Yucatan peninsula littoral, Mexico.

Taxa	References	Sample localities	Obs.
1. *Udotea abbottiorum* D. S. Littler & M. M. Littler	11Q, 20Q	9,13,28,29,31,32,34	NRC
2. *Udotea caribaea* D. S. Littler & M. M Littler	11Q, 20Q, 21Y, 24Y	26,27,30,31,32,33,34	
3. *Udotea conglutinata* (J. Ellis & Solander) J.V. Lamouroux	4Q,5Q, 6CYQ, 7Q, 8Q, 11Q, 12Q, 13Q, 15Q, 18Q,20Q, 21Y, 22CQ	25,26,27,28,30,31,32,33,34	
4. *Udotea cyathiformis* Decaisne	6CQ, 10Q, 11Q, 12Q, 13Q, 14Q, 15Q, 20Q, 22C	22	NRY
5. *Udotea cyathiformis* f. *sublittoralis* (W. R. Taylor) D. S. Littler & M.M. Littler	5Q, 6Q, 7Q, 8Q, 11Q, 12Q, 13Q, 14Q, 20Q	9,24,29,31,32,34	
6. *Udotea cyathiformis* var. *flabellifolia* D. S. Littler & M. M. Littler	25Q	8,9,11,32,34	NRC
7. *Udotea dixonii* D. S. Littler & M. M. Littler	11Q, 14Q, 18Q, 20Q, 22C	9,11,13,14,24,26,27,29,33,34	
8. *Udotea dotyi* D.S. Littler & M. M Littler	20Q	9,12,29	NRC
9. *Udotea fibrosa* D.S. Littler & M. M. Littler	20Q, 25Q	24,34	

.....continued on the next page

TABLE 3. (Continued)

Taxa	References	Sample localities	Obs.
10. *Udotea flabellum* (J. Ellis & Solander) M. A. Howe	1Q, 2CQ, 3Q, 4Q, 5Q, 6CQ, 7Q, 8Q, 9Q, 10Q, 11Q, 12Q, 13Q, 14Q, 15C, 17C, 18Q, 19Y, 20Q, 21Y, 22C	3,4,7,8,9,11,12,13,20,21,23,26,29,31,34	
11. *Udotea looensis* D.S. Littler & M. M. Littler	11Q, 14Q, 18Q, 20Q, 22C	8,9,18,26,30,31,32	NRY
12. *Udotea luna* D. S. Littler & M. M Littler	11Q, 20Q	8,9,11,25,26,28,31	NRC
13. *Udotea norrisii* D. S. Littler & M. M Littler		3,11,26,33,34	NRC NRQ
14. *Udotea occidentalis* A. Gepp & E. Gepp	5Q, 10Q, 12Q, 13Q, 14Q, 18Q, 22C		
15. *Udotea spinulosa* M.A. Howe	2C, 5Q, 9Q, 10Q, 11Q, 13Q, 18Q, 19Y, 21Y, 22C, 23C	6,11	
16. *Udotea unistratea* D. S. Littler & M. M. Littler	14Q, 17C, 18Q		
17. *Udotea wilsonii* A. Gepp, E. Gepp & M. A. Howe	6Q, 10Q, 11Q, 13Q, 14Q, 18Q, 20Q	26	

See Localities names in the Material and Methods section.

References: 1=Huerta-Múzquiz 1958; 2= Huerta-Múzquiz & Garza-Barrientos 1966; 3= Taylor 1972; 4= Garza-Barrientos 1975; 5= Huerta-Múzquiz & Garza-Barrientos 1980; 6= Huerta-Múzquiz *et al.* 1987; 7= Aguilar-Rosas *et al*. 1989; 8= Aguilar-Rosas 1990; 9= Mateo-Cid & Mendoza-González 1991; 10= Mendoza-González & Mateo-Cid 1992; 11= Collado-Vides 1993; 12= Dreckmann *et al*. 1996; 13= Aguilar-Rosas *et al.* 1998; 14= Mendoza-González *et al.* 2000; 15= Aguilar-Rosas *et al.* 2001; 16= Ortegón-Aznar *et al*. 2001; 17= Callejas-Jiménez *et al*. 2005; 18= Mateo-Cid & Mendoza-González 2007; 19= Sánchez-Molina *et al.* 2007; 20= Collado-Vides *et al.* 2009; 21= Rosado-Espinosa *et al.* 2012; 22= Mateo-Cid *et al*. 2013; 23= Mendoza-González *et al*. 2013; 24= Ortegón & Perera 2014, 25= Acosta-Calderón *et al*. 2016.

Q, Quintana Roo; Y, Yucatan; C, Campeche

Observations (Obs.): NRC, New record Campeche; NRY, New record Yucatán; NRQ, New record Quintana Roo

Distribution

The genus *Udotea* shows a discontinuous distribution along the Yucatan peninsula littoral. In the shores of Quintana Roo, *Udotea* species were present in all sampled localities, towards the Yucatan coast a few specimens were found, and in the boundaries between Yucatan and Campeche no species were recorded. Finally, some taxa were found in the middle of the Campeche coastline, and in the limits with Tabasco no specimens of this genus were obtained (Fig. 1). Regarding the distribution by species, *Udotea flabellum* (J. Ellis & Solander) M.A. Howe and *Udotea dixonii* D.S. Littler & M.M. Littler were widely distributed in the Yucatan peninsula littoral. Both species were located in shallow subtidal environments (to 5 m depth) with water movement or protected areas, on rocky platforms and sandy bottoms associated with sea grass meadows (Fig. 2). *Udotea abbottiorum , U. looensis,* and *U. luna* were found in several localities along the Yucatan peninsula shore, in areas with sandy bottoms associated to sea grass meadows, subtidal rocky platforms exposed to the swell, and rocky-sandy substrata in reef lagoons (Quintana Roo), as well as in zones with turbid water and sandy and rocky bottoms (Yucatan), or in beaches with sandy bottoms with sea grass and rocky platforms with little water movement (Campeche), whereas, *Udotea caribaea* D.S. Littler & M.M. Littler and *Udotea conglutinat*a (J. Ellis & Solander) J.V. Lamouroux were present only in the Quintana Roo shore, in shallow zones (to 1.5 m depth) with rocky bottom and exposed to waves (Fig. 3). *Udotea cyathiformis* f. *sublittoralis* (W.R. Taylor) D.S: Littler & M.M. Littler, *U. cyathiformis* var. *flabellifolia* and, *U. norrisii* were found in subtidal rocky platforms exposed to the swell, and beaches with sandy bottoms with sea grass (Fig. 4). *Udotea cyathiformis, U. dotyi, Udotea fibrosa* D.S. Littler & M.M Littler*, Udotea spinulosa* M. Howe*,* and *Udotea wilsonii* A. Gepp, E. Gepp & M. Howe were uncommon species in the study area, in habitats with rocky bottom and protected from waves (Fig. 5). Finally, *U. occidentalis* have been recorded for Chankanab, Cozumel Island at 15 m depth and *U. unistratea* for the Campeche coast in Don Lin locality (Fig. 6).

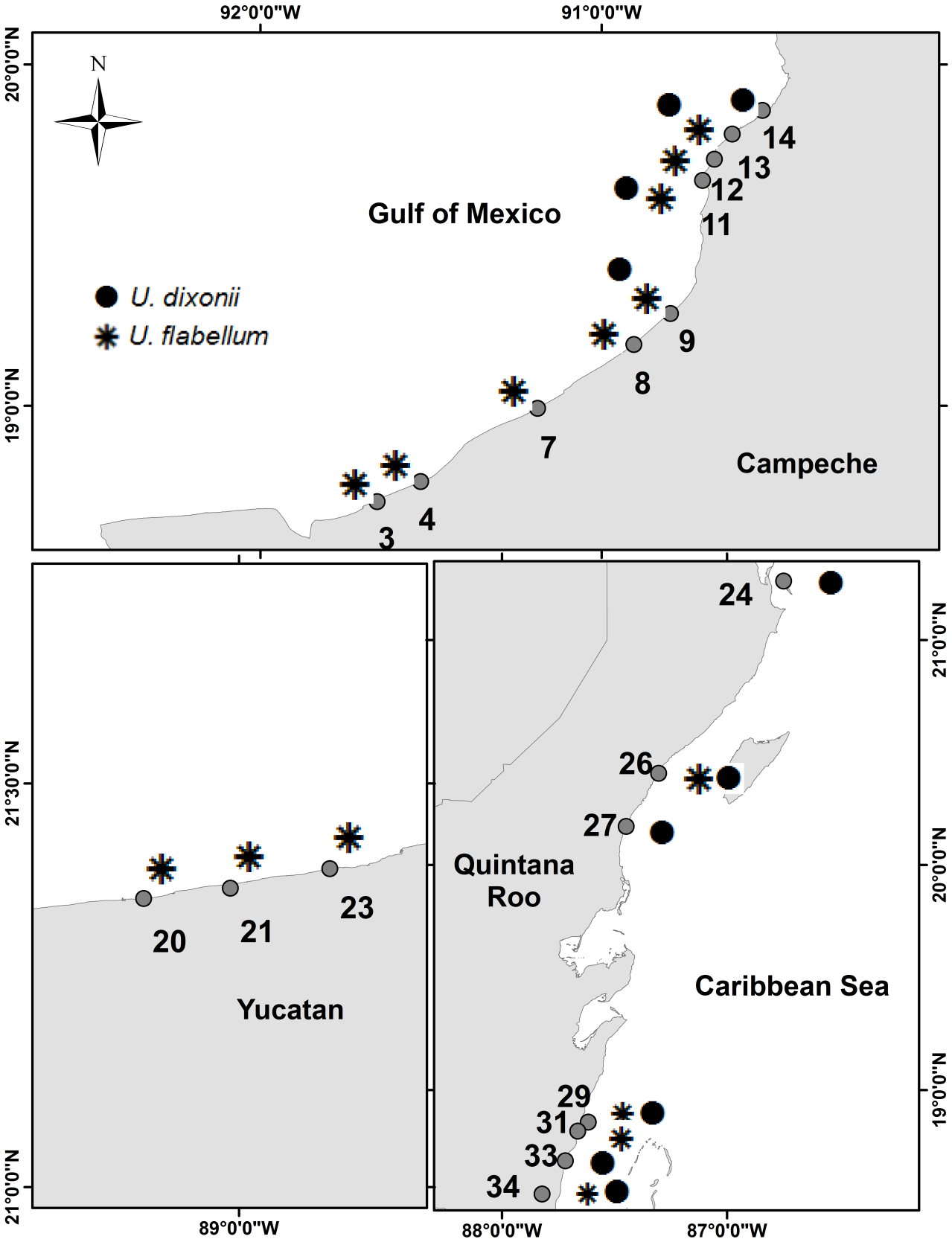


FIGURE 2. Distribution of *U. flabellum* and *U. dixonii* in the study area.

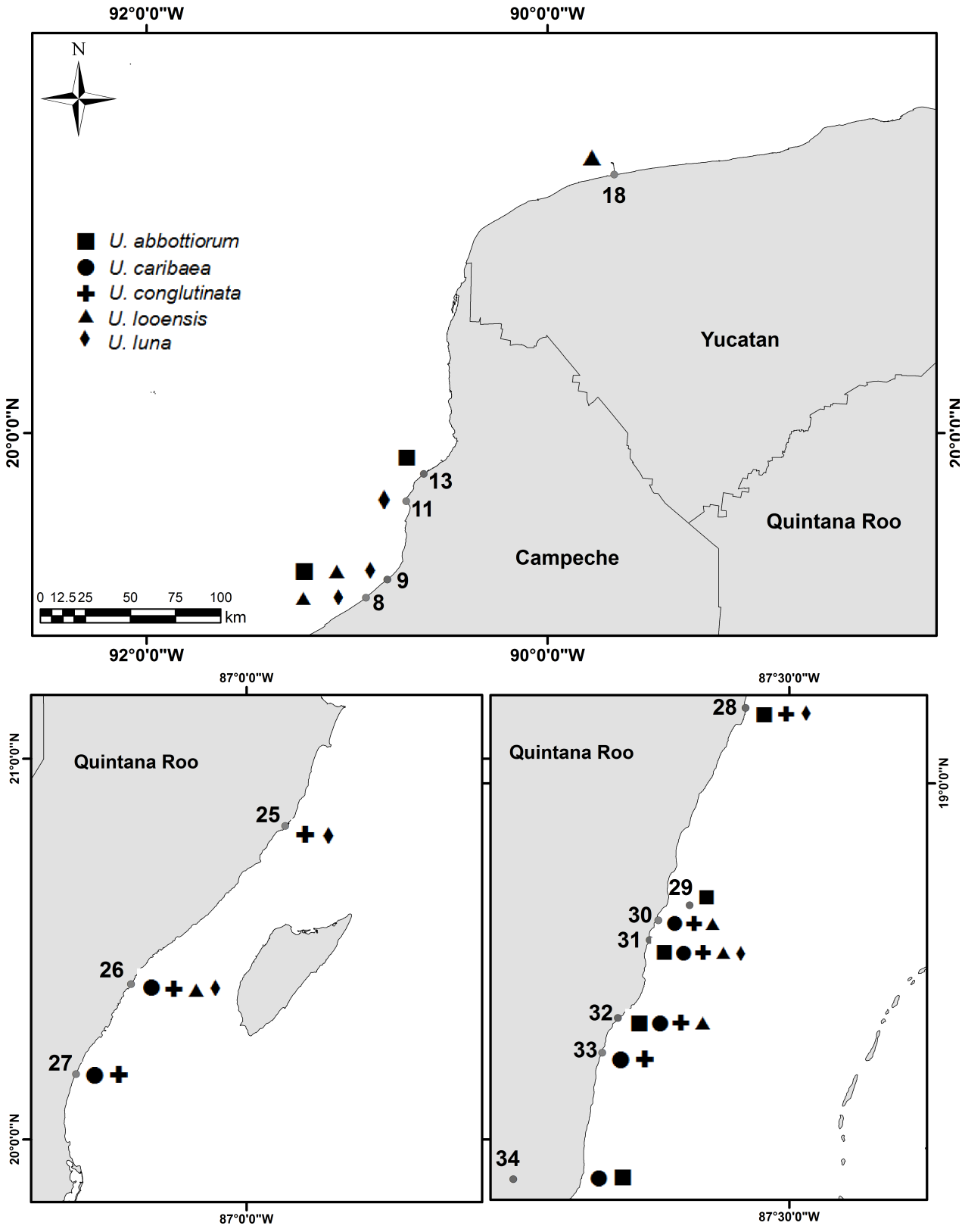


FIGURE 3. Distribution of *Udotea abbottiorum*, *U. caribaea*, *U. conglutinata*, *U. looensis,* and *U. luna*

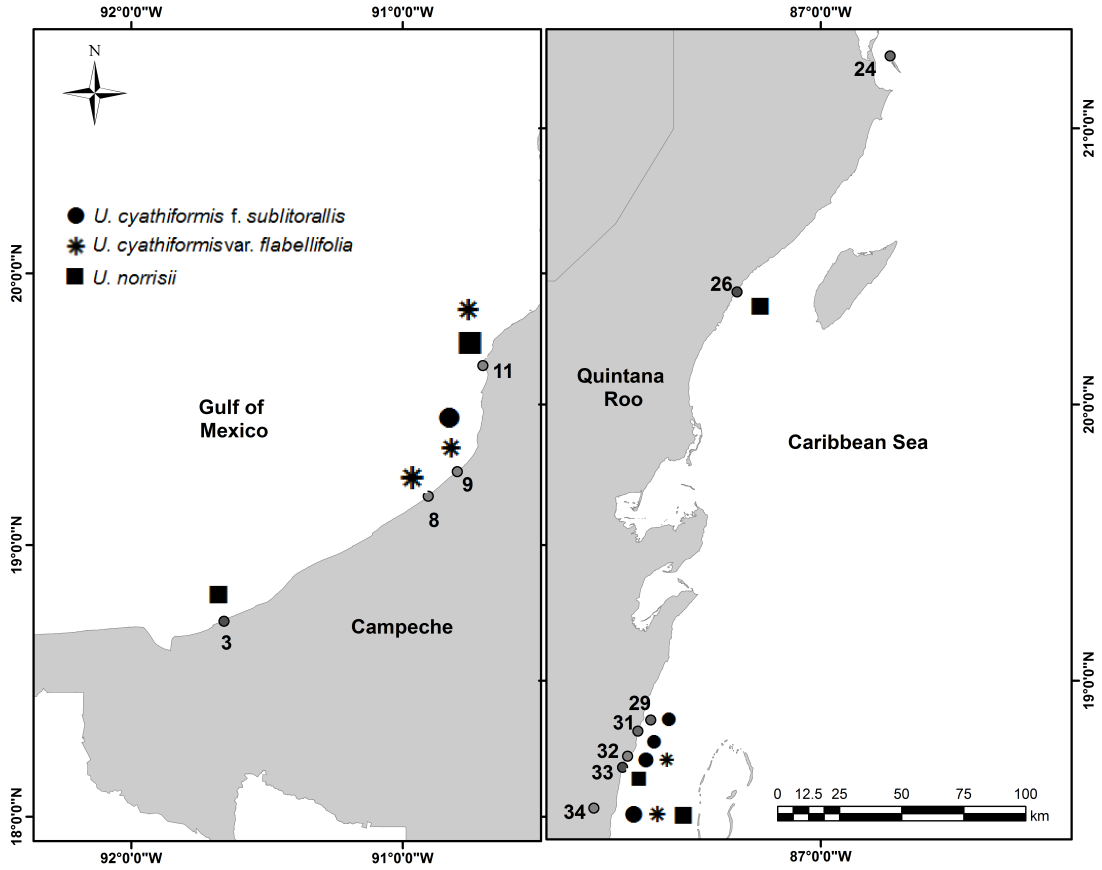


FIGURE 4. Distribution of *U. cyathiformis* f. *sublittoralis, U. cyathiformis* var. *flabellifolia,* and *U. norrisii* in the study area

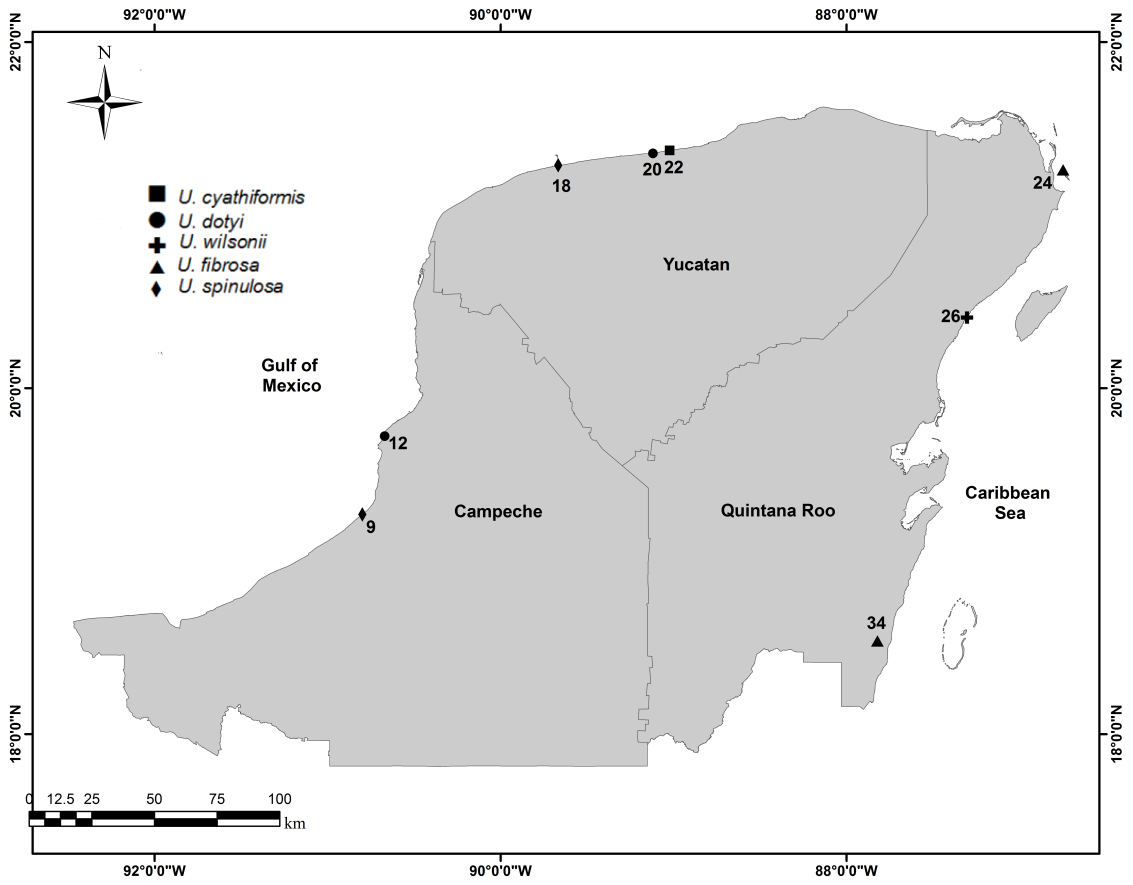


FIGURE 5. Distribution of *U. cyathiformis, U. dotyi, U. fibrosa, U. spinulosa,* and *U. wilsonii* in the study area

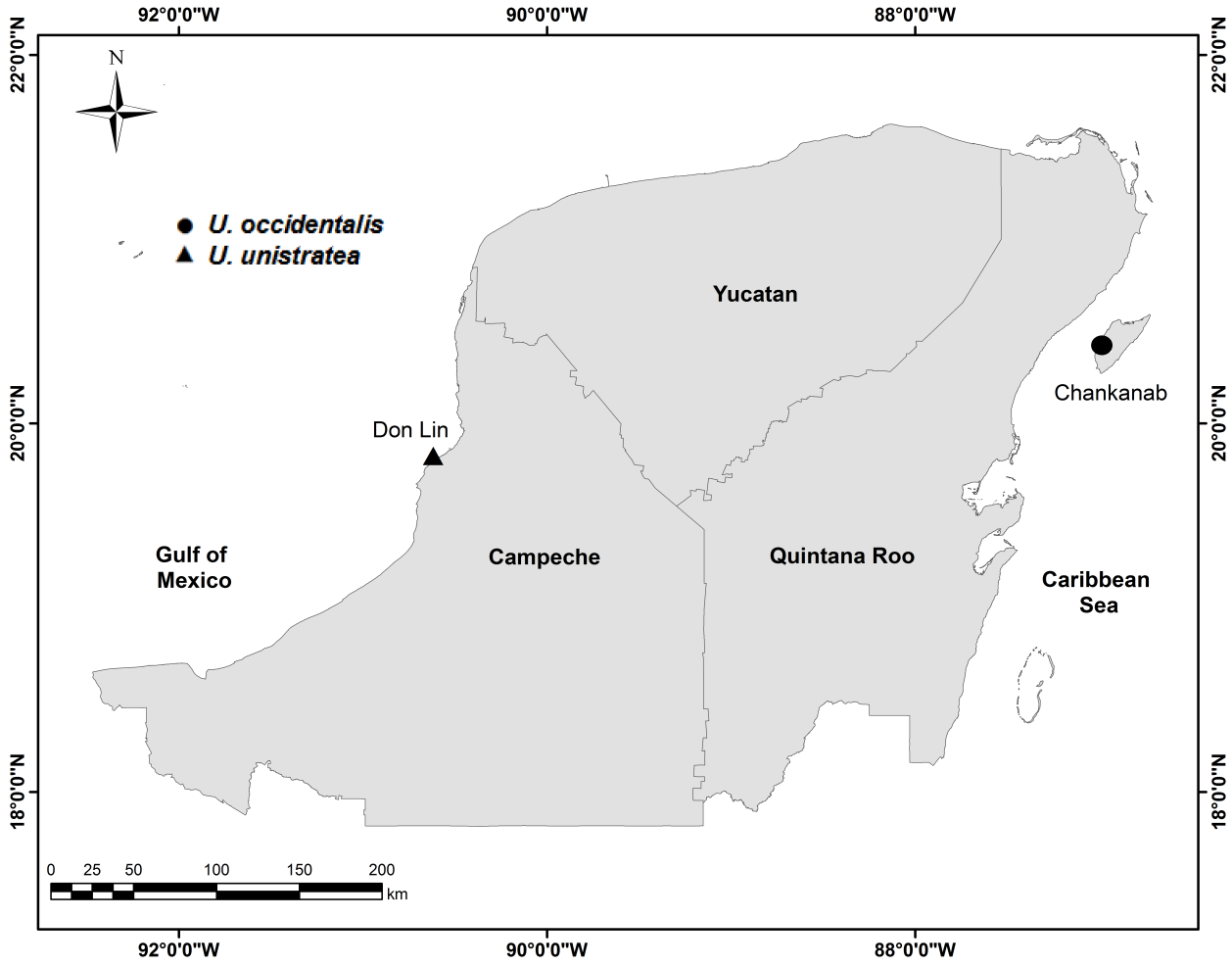


FIGURE 6. Distribution of *U. occidentalis*, and *U. unistratea* in the study area

Taxonomic descriptions

It was observed that qualitative characteristics are more important for the determination of *Udotea* species than quantitative characters. The presence of lateral appendages on blade siphons separated the species into two main groups: first, those species that have no appendages or ecorticate: *U. abbottiorum*, *U. caribaea*, *U. conglutinata*, *U. cyathiformis*, *U. cyathiformis* f. *sublittoralis*, *U. cyathiformis* var. *flabellifolia*, *U. fibrosa*, *U. looensis*, *U. luna*, *U. unistratea*; and second, those with lateral appendages on the blade siphons (corticate): *U dixonii*, *U. dotyi*, *U. flabellum*, *U. norrisii, U. occidentalis, U. spinulosa,* and *U. wilsonii*. The ecorticate species are clearly distinguishable by several characteristics of the blade and the appendage stipe morphology. In contrast, the corticate species show high similarity in the shape of the blades and stipe. The arrangement and shape of the blade and stipe siphons allowed assignment to a specific epithet. Morphological and anatomical characters of the 17 *Udotea* taxa records in this study are summarized in Table 4 and Table 5 and the taxonomic descriptions follows.

TABLE 4. Morphological characters of 17 taxa of *Udotea* found in the Yucatan peninsula littoral. Taxa: 1). *U. abbottiorum*, 2) *U. caribaea*, 3) *U. conglutinata*, 4) *U. cyathiformis*, 5) *U. cyathiformis* f. *sublittoralis*, 6*) U. cyathiformis* var. *flabellifolia*, 7) *U. dixonii*, 8) *U. dotyi*, 9) *U. fibrosa*, 10) *U. flabellum*, 11) *U. looensis*, 12) *U. luna*, 13) *U. norrisii*, 14) *U. occidentalis*, 15) *U. spinulosa*, 16) *U. unistratea*, 17) *U. wilsonii*. Characters: a) Shape blade, b) Blade zonation (+, present; -, no present), c) Blade lower margin, d) Blade type (M, multistratose; U, unistratose), e) blade superior margin (M, multistratose; U, unistratose), f) Transition stipe-blade (E, evident; G, gradual; NE, not evident), g) Blade appendages shape, h) Stipe appendages shape. NA) Not applicable.

Taxa	Morphological characters							
	a	b	c	d	e	f	g	h
1	flabellate	+	truncate	M	M	E	NA	swollen
2	orbiculate	+	truncate/ ovalate	M	M	G	NA	small digitate
3	flabellate-reniform	+	ovalate-reniform	M	M	G	NA	swollen digitate
4	spatulate		acute	M	M	E	NA	asymmetrical dichotomies, with swollen or flattened apices
5	spatulate	+	ovalate	M	M	E	NA	short swollen and flattened
6	flabellate	+	obtuse	M	M	E	NA	distorted digitate
7	spatulate	+	ovalate	M	M	NE	many, swollen knobs of short projection	stubby, digitate projections
8	flabellate	+	ovatate-truncate	M	M	NE	irregular flat apices	numerous blunt rounded tips
9	spatulate	-	ovalte	M	M	E	NA	swollen
10	flabellate	+	ovate-truncate	M	M	NE	branched projections, apices swollen and flat	dichotomously small tips
11	orbiculate-reniform	+	ovalate-reniform	M	U	E	NA	abundant dichotomously lanceolate apices
12	orbiculate-reniform	+	ovalate-reniform	M	M	G	NA	dichotomously acute and lanceolate apices.
13	flabellate-spatulate	+	ovalate-truncate	M	M	NE	small swollen and flat dichotomously apices	swollen tips
14	flabellate	+	reniform	M	M	G	unique knobs with appearances of sunken	numerous rounded projections
15	spatulate-flabellate	+	obtuse-acute	M	U	G	spine-like projection	long, acute, digitate projections
16	flabellate	+	acute	U	U	E	NA	short dichotomously lobed, blunt tips
17	flabellate-reniform	+	ovalate-reniform	M	M	G	short and knobby	short swollen and flattened dichotomous tips

TABLE 5. Anatomical characters used to delimit the 17 *Udotea* taxa found in this study. Taxa: 1). *U. abbottiorum*, 2) *U. caribaea*, 3) *U. conglutinata*, 4) *U. cyathiformis*, 5) *U. cyathiformis* f. *sublittorali*s, 6) *U. cyathiformis* var. *flabellifolia,* 7) *U. dixonii*, 8) *U. dotyi*, 9) *U. fibrosa*, 10) *U. flabellum*, 11) *U. looensis*, 12) *U. luna*, 13) *U. norrisii*, 14) *U. occidentalis*, 15) *U. spinulosa*, 16) *U. unistratea*, 17) *U. wilsonii*. Characters: i) Blade siphons diameter, j) Distance between dichotomies, h) constriction supradichotomic diameter, k) constriction supradichotomic large, l) Blade appendages peduncles diameter, m) Blade appendages peduncles large, n) Stipe siphons diameter, o) Stipe appendages peduncle diameter, p) Stipe appendages peduncle large. NA) Not applicable.

Taxa	Anatomical characters (µm)								
	i	j	h	k	l	m	n	o	p
1	45–55	700–2300	23–27	12–24	NA	NA	58–37	20–65	160–500
2	24–80	550–1100	7–24	14–21	NA	NA	40–58	22–48	111–247
3	27–40	500–900	8–11	19–29	NA	NA	30–55	25–45	115–250
4	45–55	500–900	20–22	20–30	NA	NA	70–100	40–42	200–250
5	40–80	1200–1900	10–22	18–30	NA	NA	40–70	25–40	150–200
6	45–55	1300–2500	15–25	19–27	NA	NA	50–74	25–40	70–250
7	22–40	NA	NA	NA	12–24	60–160	22–68	20–45	140–525
8	20–40	NA	NA	NA	15–30	60–120	40–70	20–40	150–300
9	50–70	NA	15–17	18–23	NA	NA	27–47	20–30	90–150

.....continued on the next page

TABLE 5. (Continued)

Taxa	Anatomical characters (µm)								
	i	j	h	k	l	m	n	o	p
10	20–30	NA	NA	NA	13–18	85–120	30–50	30–50	180–280
11	35–55	700–1600	12–24	30–40	NA	NA	40–60	20–40	60–120
12	33–55	900–1600	9–15	25–40	NA	NA	33–63	10–45	20–120
13	20–30	NA	NA	NA	13–18	90–120	25–45	19–25	100–160
14	30–40	NA	NA	NA	10–20	40–65	30–60	20–30	150–300
15	30–45	1500–1600	NA	NA	NA	NA	45–60	20–25	40–80
16	30–60	2000–8000	20–25	20–30	NA	NA	50–80	30–40	120–300
17	43–45	NA	NA	NA	19–25	NA	45–60	20–25	120–160

Udotea abbottiorum D.S. Littler & M.M. Littler 1990:10

Type Locality:—USA, Content Keys, Monroe County, Florida.

Morphology:—Thalli to 10 cm tall, anchored on substrata by a small bulbous mass of entangled rhizoidal siphons. Stipe cylindrical lightly calcified in lower half (4–11 mm long, 2–4 mm in diameter), the upper half flattened (6–16 mm long, 4–15 mm in diameter), forming an evident transition between the stipe and blade. Blade fan-shaped, green, longer (2–9 cm) than wider (1–9 cm), lower margin obtuse o truncate, multistratose, ecorticate (no lateral appendages), lightly calcified, and zonate (Figs. 7, 8, 9).

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 45–55 µm in diameter, distance between each dichotomy ranges from 700 to 2300 µm, supradichotomic constrictions 12–24 µm length, 23–27 µm in diameter (Fig. 10). Stipe siphons adjacent to lateral appendages 37–58 µm in diameter, appendages peduncle 160–500 µm length, 20–65 µm in diameter, sometimes constriction at the base. Appendages dichotomously branched 2–4 times, with swollen tips (Fig. 11).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Pulticub, 14 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23086. MEXICO. Quintana Roo, Uvero, 13 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23087. MEXICO. Quintana Roo, Punta Mahahual, 13 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23090. MEXICO. Quintana Roo, Santa Rosa, 12 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23091. MEXICO. Quintana Roo. Rio Indio, 19 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23085. MEXICO. Campeche, Playa Villamar, 25 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23089. MEXICO. Campeche, Lerma, 23 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23088. Campeche, Carretera a Campeche km 732, 9-05-1966, A. Vargas, ENCB 16773.

Geographic distribution:—Florida, Bermuda, Belize, Panama, Puerto Rico, Colombia, Brazil, Mexico.

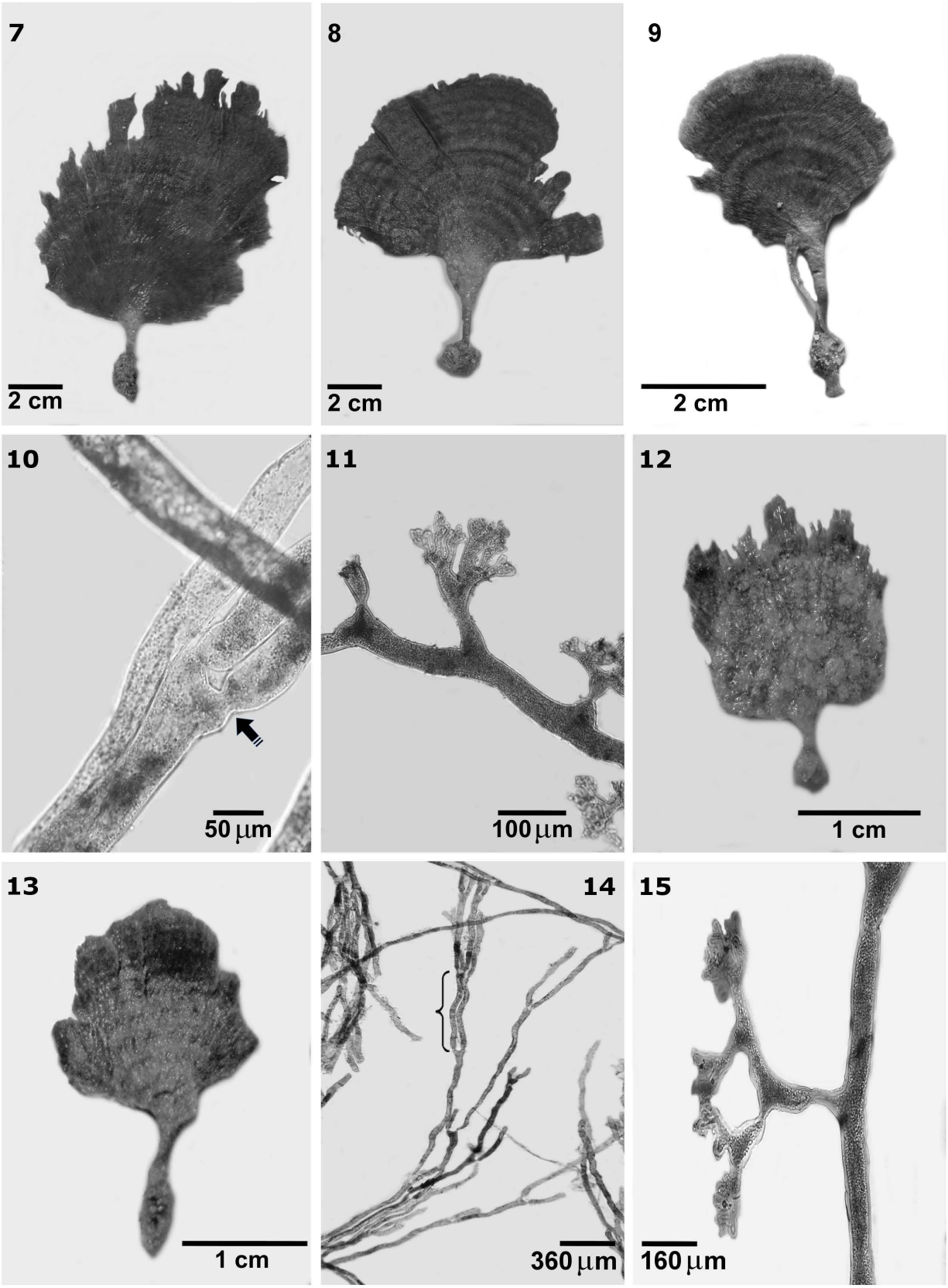
Habitat:—Sandy bottom with seagrass meadows and rock shelf with soft waves. Subtidal to 2 m deep.

Comments:—The shape of the stipe appendages and the presence of a cylindrical section shorter than the flattened portion of the stipe agrees with those described by Littler & Littler (1990). However, the diameters of stipe and blade siphons are less than those recorded in specimens from Florida, USA (Littler & Littler 1990), and Puerto Morelos, Quintana Roo, Mexico (Collado-Vides *et al*. 2009). In the Yucatan peninsula, this species has been registered only for Puerto Morelos (Collado-Vides *et al*. 2009), so in this paper the distribution of *U. abbottiorum* is extended to the Quintana Roo coast and is recorded for the first time for the Campeche shoreline.

Udotea caribaea D.S. Littler & M.M. Littler 1990:211

Type Locality:—BELIZE, Northwest side of Tobacco Range.

Morphology:—Thalli to 3.5 cm tall, anchored on substrata by a small compact mass of entangled rhizoidal siphons. Stipe cylindrical, 3–11 mm length, 1–3 mm wide. Gradual transition between the stipe and blade. Blade orbiculate, light green, longer (1–3 cm) than wider (1.5–3.5 cm), lower margin ovate or truncate, multistratose, ecorticate, and heavily calcified. Blade zonation present, although sometimes not evident due to the growth of epiphytic algae on the blade (Figs. 12, 13).



FIGURES 7–11. *U. abbottiorum*. 7–9) external morphology, 10) blade siphon and detail of the supradichotomic constriction, 11) lateral appendages of the stipe. **FIGURES 12–15**. *U. caribaea*. 12–13) external morphology, 14) blade siphon showing the distance between dichotomies, 15) lateral appendages of the stipe.

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 24–80 µm in diameter, distance between each dichotomy varies from 550 to 1100 µm, supradichotomic constrictions 14–21 µm length, 7–24 µm in diameter (Fig. 14). Stipe siphons adjacent to lateral appendages 40–85 µm in diameter, appendages peduncle 111–247 µm length, 22–48 µm in diameter. Appendages dichotomously branched 2–3 times, with small digitate tips (Fig. 15).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Santa Rosa, 9 September 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23097. MEXICO. Quintana Roo, Punta Piedra, 17 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23094. MEXICO. Quintana Roo, Punta Rio Bermejo, 12 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23093. MEXICO. Quintana Roo, Rio Indio, 13 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23092. MEXICO. Quintana Roo, Isla Mujeres, 16 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23095. MEXICO. Quintana Roo, Punta Mahahual, 10 September 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23096. MEXICO. Quintana Roo, Punta Akumal, 12 September 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23098. MEXICO. Quintana Roo. Pulticub, 14 September 2012, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 20817. MEXICO. Quintana Roo, Punta Pelicanos, 20 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 22849.

Geographic distribution:—Bermuda, Belize, Panama, Cuba, Martinique, Puerto Rico, Brazil, Mexico.

Habitat:—Subtidal rocky platforms with moderate surge.

Comments:—The shape of the stipe appendages agrees with those described by Littler & Littler (1990). Regarding the dimensions of the blade and stipe siphons, the thalli examined show a wider range than those recorded in specimens from Belize (Littler & Littler 1990), but coincide with those recorded in thalli from Puerto Morelos, Quintana Roo, Mexico (Collado-Vides *et al*. 2009). In this paper, the wide distribution of this species is confirmed in the Quintana Roo littoral.

Udotea conglutinata (J. Ellis & Solander) J.V. Lamouroux 1816: 312

Basionym: *Corallina conglutinata* J. Ellis & Solander 1786: 125

Type Locality:—BELIZE. Northwest side of Tobacco Range.

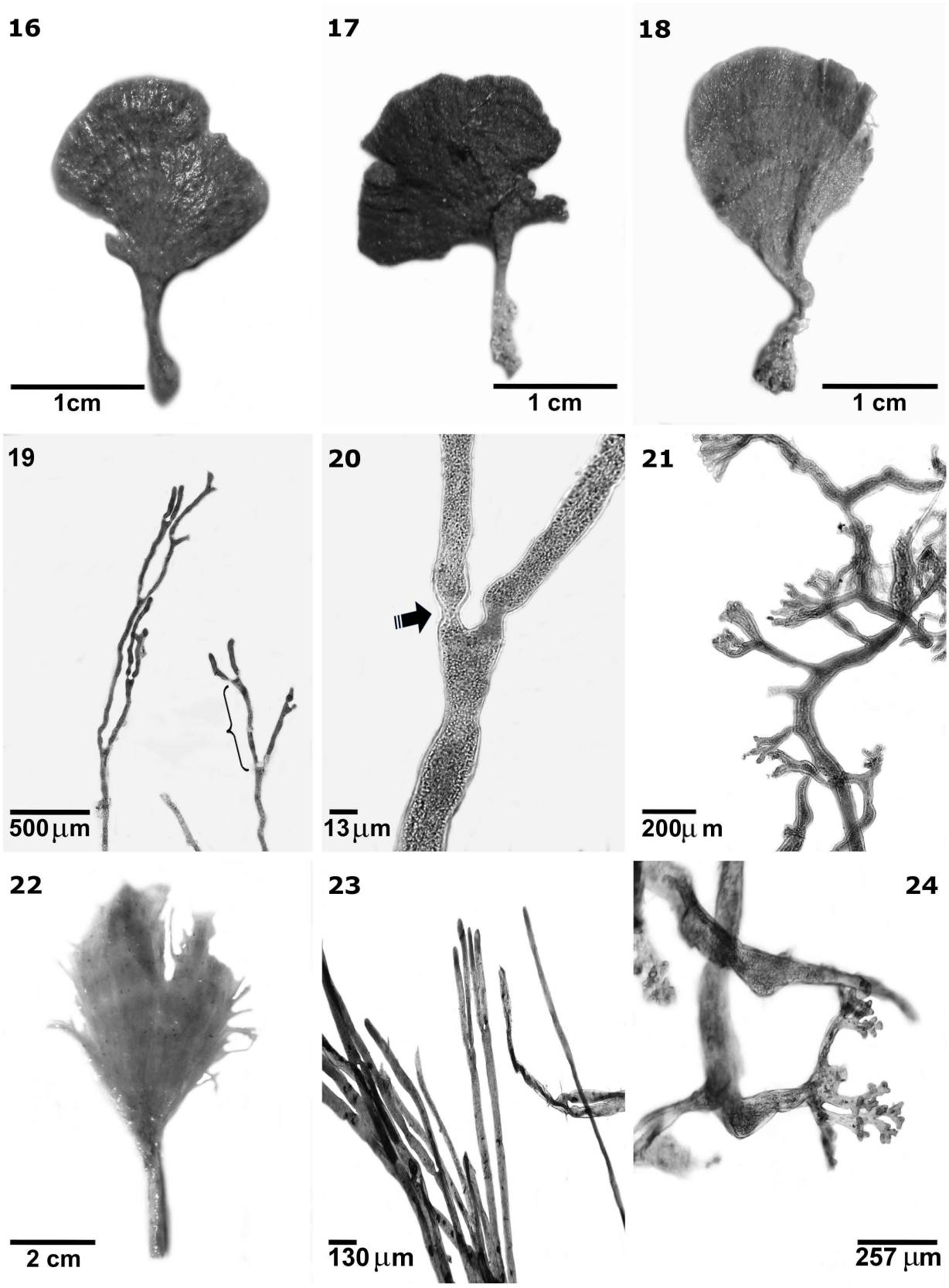
Morphology:—Thalli to 4 cm tall, anchored to the substrata by a small fibrous rhizoidal mass. Stipe cylindrical 3–15 mm length, 1–3 mm diameter, and flattening towards the blade. Gradual transition between the stipe and blade. Blade fan-shaped, olive green, longer (1.5–3 cm) than wider (1.4–3 cm), lower margin ovate, truncate or cordate, multistratose, ecorticate, zonate, and heavy calcified except in superior margin (Figs. 16, 17, 18).

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 27–40 µm in diameter, with apices distinct torulous and contorted (Fig. 19). Distance between each dichotomy varies from 500 to 900 µm, supradichotomic constrictions 19–29 µm length, 8–11 µm in diameter (Fig. 20). Stipe siphons adjacent to lateral appendages 30–55 µm in diameter, appendages peduncle 115–250 µm length, 25–45 µm in diameter. Appendages dichotomously branched 2–3 times, and ending in dichotomies (Fig. 21).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Punta Piedra, 17 December 2014, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 23119. MEXICO. Quintana Roo, Punta Rio Bermejo, 12 April 2015, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 23115. MEXICO. Quintana Roo, Isla Mujeres, 16 June 2014, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 23117. MEXICO. Quintana Roo, Punta Mahahual, 20 December 2014, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 23114. MEXICO. Quintana Roo, Punta Akumal, 15 April 2015, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 23113. MEXICO. Quintana Roo, Pulticub, 14 April 2015, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 23116. MEXICO. Quintana Roo, Puerto Morelos, 15 June 2014, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 23118. MEXICO. Quintana Roo, Pulticub, 14 September 2012, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 20855. MEXICO. Quintana Roo, Cayo Valencia, 18 January 2011, L.E. Mateo Cid, A.C. Mendoza González, J.A. Acosta Calderón, ENCB 19840. MEXICO. Quintana Roo, Playa Lancheros, Isla Mujeres, 1 November 1984, L.E. Mateo Cid, A.C. Mendoza González, ENCB 6125. MEXICO. Quintana Roo, Puerto Morelos, 21 May 1993, L.E. Mateo Cid, A.C. Mendoza González ENCB 17218. MEXICO. Campeche, Lerma, 21 January 1966, A. Vargas, ENCB 16774.

Geographic distribution:—Bahamas, Bermuda, Florida, Panama, Jamaica, Puerto Rico, Cuba, Virgin Islands, Brazil, Colombia, Venezuela, Indonesia, Mexico.



FIGURES 16–21. *U. conglutinata*. 16–18) external morphology, 19) blade siphon showing the torulous apices, 20) detail of the supradichotomic constriction, 21) stipe lateral appendages. **FIGURES 22–24**. *U. cyathiformis*. 22) external morphology, 23) blade siphon apices, 24) lateral appendages of the stipe.

Habitat:—Calcareous rock and rocky platforms with soft waves. Subtidal to 4 m depth.

Comments:—The first morphological description of this species was made by J. Ellis & Solander (1786), as *Corallina conglutinata*. Later, J.V Lamouroux (1816) made the change from *C. conglutinata* to *Udotea conglutinata*. These descriptions were made with specimens from the Bahamas and mentioned a fibrous root, a simple stem and a fan shaped, made up of dichotomous branches covered by a calcareous substance. Howe (1909) and Taylor (1960) presented more detailed descriptions of the morphology of the blade and stipe; the lateral appendages of the stipe siphons also provide information about the diameter of the blade siphons. In the work of Littler & Littler (1990) more precise description and illustrations are presented about the shape of the apices of the blade siphons and the lateral appendages of the stipe siphons. The shape of the tips of the blade siphons is distinctive in this species. The shape and dimensions of the stipe appendages correspond to those registered for specimens from Bahamas, Florida and Puerto Rico (Howe 1909, Taylor 1960, Littler & Littler 1990), and the Mexican Caribbean (Collado-Vides *et al*. 2009). Regarding the dimensions of the blade and stipe siphons, the thalli examined show dimensions smaller than those recorded in specimens from Bahamas, Florida, Jamaica (Howe 1909, Taylor 1960) and Belize (Littler & Littler 1990), but coincide with those recorded in thalli from Puerto Morelos, Quintana Roo, Mexico (Collado-Vides *et al*. 2009). The wide distribution of this species is confirmed in the Quintana Roo littoral, although no specimens were found in Dzilam de Bravo, Yucatan, as mentioned by Rosado-Espinosa *et al*. (2011), as well as in Lerma, Campeche (Mateo-Cid *et al*. 2013).

Udotea cyathiformis Decaisne 1842: 106

Type Locality:—FRANCE, Iles des Saintes, Guadeloupe, Lesser Antilles.

Morphology:—Thalli to 4.5 cm tall, anchored on substrata by a small fibrous rizoidal mass. Stipe cylindrical, tinny 13 mm length, 2 mm diameter. Evident transition between stipe and blade. Blade spatulate, light green, delicate, longer (2.9 cm) than wider (1.5 cm), acute lower margin, multistratose, ecorticate, lightly zonate and calcified (Fig. 22).

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 45–55 µm in diameter (Fig. 23), distance between each dichotomy varies from 500 to 900 µm, supradichotomic constriction 20–30 µm length, 20 µm in diameter. Stipe siphons adjacent to lateral appendages 70–100 µm in diameter, appendages peduncle 200–250 µm length, 40 µm in diameter, appendages irregularly branched, terminating in asymmetrical dichotomies, with swollen or flattened apices (Figs. 24, 25).

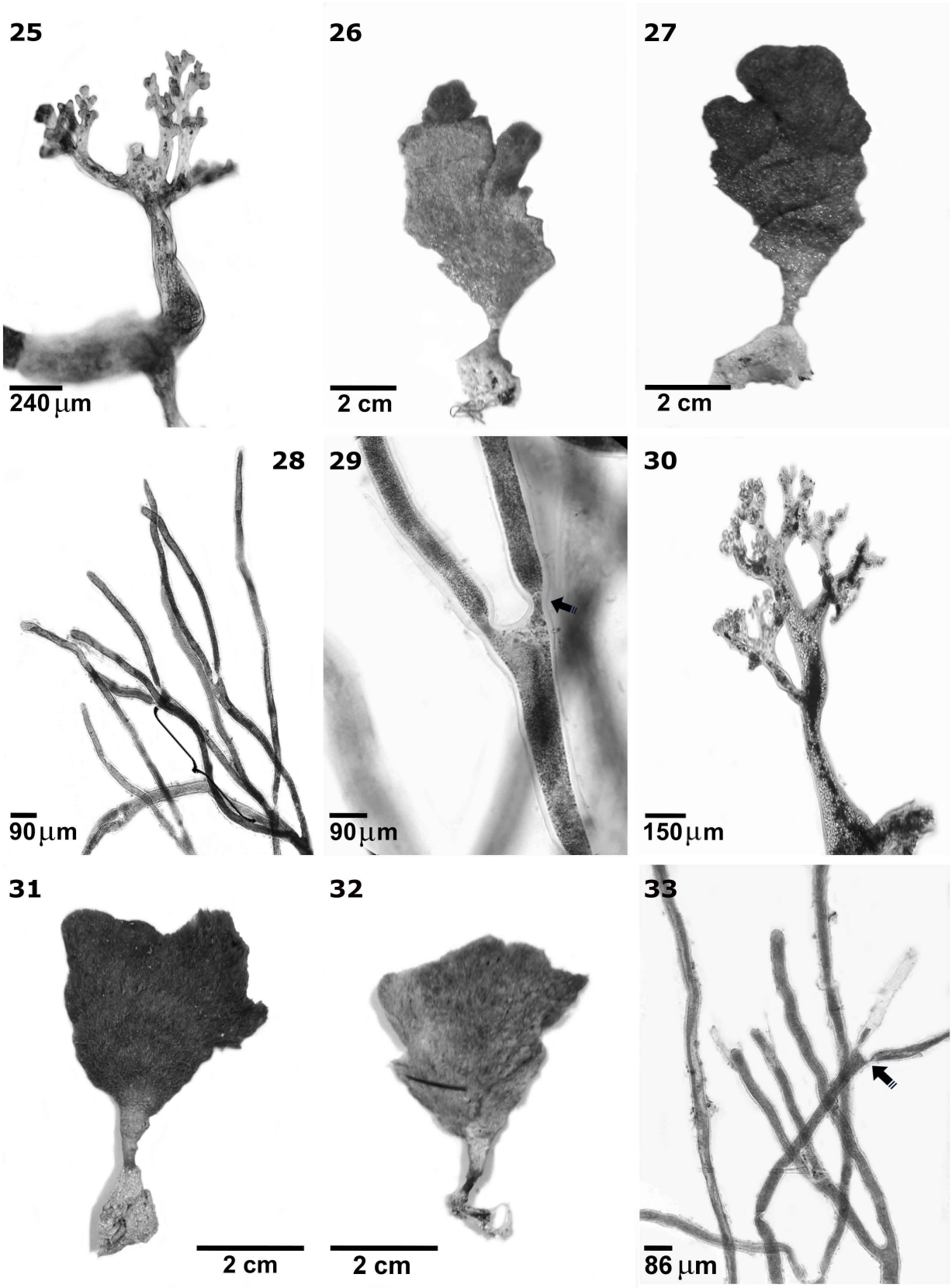
Reproduction:—Vegetative

Material examined:—MEXICO. Yucatan, Santa Clara, 26 June2011, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23099. MEXICO. Quintana Roo, Arrecife Colombia, Isla Cozumel, 14 September 1993, R.B. Searles, R. Robles, ENCB 12759. MEXICO. Quintana Roo, Arrecife Santa Rosa, Isla Cozumel, 02 June1996. R. Robles, E. Caister, M. Volovsek, ENCB 12745.

Geographic distribution:—Bermuda, Florida, North Carolina, Texas, Belize, Panama, Bahamas, Barbados, Cuba, Haiti, Guadeloupe, Jamaica, Lesser Antilles, Puerto Rico, Virgin Islands, Brazil, Venezuela, South China Sea, Mexico.

Habitat:—Rocky platforms subtidal to 2 m depth.

Comments:—Decaisne (1842) described for the first time this species, assigned the epithet of cyathiformis for its cup shaped frond (cyathis) and a cylindrical stipe. The description was made with specimens from the Antilles, but the author did not show any illustrations. Howe (1909) presented a more detailed description of the morphology of the blade, blade siphons, and the lateral appendages of the stipe siphons, also add information about the diameter of the blade siphons. In the work of Littler & Littler (1990) more precise description and illustrations are presented about the shape of the apices of the blade siphons and the lateral appendages of the stipe siphons. *Udotea cyathiformis* has been characterized by a cup shaped blade (Decaisne 1842, Howe 1909, Littler & Littler 1990, Collado-Vides *et al.* 2009), however in this study the revised specimen shows a spatulate blade with an acute lower margin. The shape of stipe appendages agrees with those described by Littler & Littler (1990), and the dimensions of blade and stipe siphons are also consistent with description of Littler & Littler (1990) and Collado-Vides *et al*. (2009). The presence of this taxon could not be confirmed by the collection in Quintana Roo littoral, as mentioned by Huerta-Múzquiz *et al*. (1987), Mendoza-González & Mateo-Cid (1992), Dreckmann *et al*. (1996), Aguilar-Rosas *et al*. (1998), Mendoza-González *et al*. (2000), Aguilar-Rosas *et al*. (2001) and Collado-Vides *et al.* (2009), neither in the Campeche shoreline (Mateo-Cid *et al*. 2013), possibly because this species is distributed at depths greater than those sampled in this study and only one specimen was obtained from the Yucatan coast. *Udotea cyathiformis* is recorded for the first time for the Yucatan littoral.



FIGURES 25. *U. cyathiformis*. 25) stipe lateral appendages. **FIGURES 26–30**. *U. cyathiformis* f. *sublittoralis*. 26–27) external morphology, 28) blade siphon showing the distance between dichotomies, 29) detail of the constriction supradichotomic, 30) lateral appendages of the stipe. **FIGURES 31–33**. *U. cyathiformis* var. *flabellifolia*. 31–32) external morphology, 33) blade siphon apices and detail of the constriction supradichotomic.

Udotea cyathiformis* f. *sublittoralis (W.R. Taylor) D.S. Littler & M.M. Littler 1990: 216
Basionym:—*Udotea sublittoralis* W.R. Taylor 1928: 91

Type Locality:—USA. Florida, Garden Key, Dry Tortugas.

Morphology:—Thalli to 12 cm tall, anchored on substrata by a compact rhizoidal mass. Stipe cylindrical 5–47 mm length, 3–6 mm diameter and flattening towards the blade. Evident transition between the stipe and blade. Spatulate blade, green, longer (1–8 cm) than wider (1.5–5 cm), lower margin ovate, multistratose, ecorticate, calcified, and lightly zonate (Figs. 26, 27).

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 40–80 µm in diameter, distance between each dichotomy ranges from 1200 to 1900 µm (Fig. 28), supra dichotomous constrictions 18–30 µm length, 10–20 µm in diameter (Fig. 29). Stipe siphons adjacent to lateral appendages 40–70 µm in diameter, appendages peduncle 150–200 µm length, 25–40 µm in diameter. Appendages dichotomously branched 2–3 times, with short swollen and flattened apices (Fig. 30).

Reproduction:—Vegetative.

Material examined:—MEXICO. Quintana Roo, Santa Rosa, 11 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23100. MEXICO. Quintana Roo, Santa Rosa, 9 September 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23105. MEXICO. Quintana Roo, Santa Rosa, 18 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23122. MEXICO. Quintana Roo, Isla Mujeres, 16 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González ENCB, 23120. MEXICO. Quintana Roo, Rio Indio, 11 September 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23101. MEXICO. Quintana Roo, Punta Akumal, 16 December 2014 J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23121. MEXICO. Quintana Roo, Punta Placer, 13 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23106. MEXICO. Quintana Roo, Uvero, 10 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23102. MEXICO. Quintana Roo, Punta Mahahual, 20 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23104. MEXICO. Quintana Roo, Pulticub, 14 September 2012, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González ENCB 20854. MEXICO. Quintana Roo, Punta Pelicanos, 17 January 2011, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 20707. MEXICO. Campeche, Playa Villamar, 25 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23103.

Geographic distribution:—Florida, Lesser Antilles, Brazil, North Carolina, Belize, Panama, Bahamas, Cuba, Martinique, Puerto Rico, Mexico.

Habitat:—Rocky platforms with soft waves. Subtidal to 2 m depth.

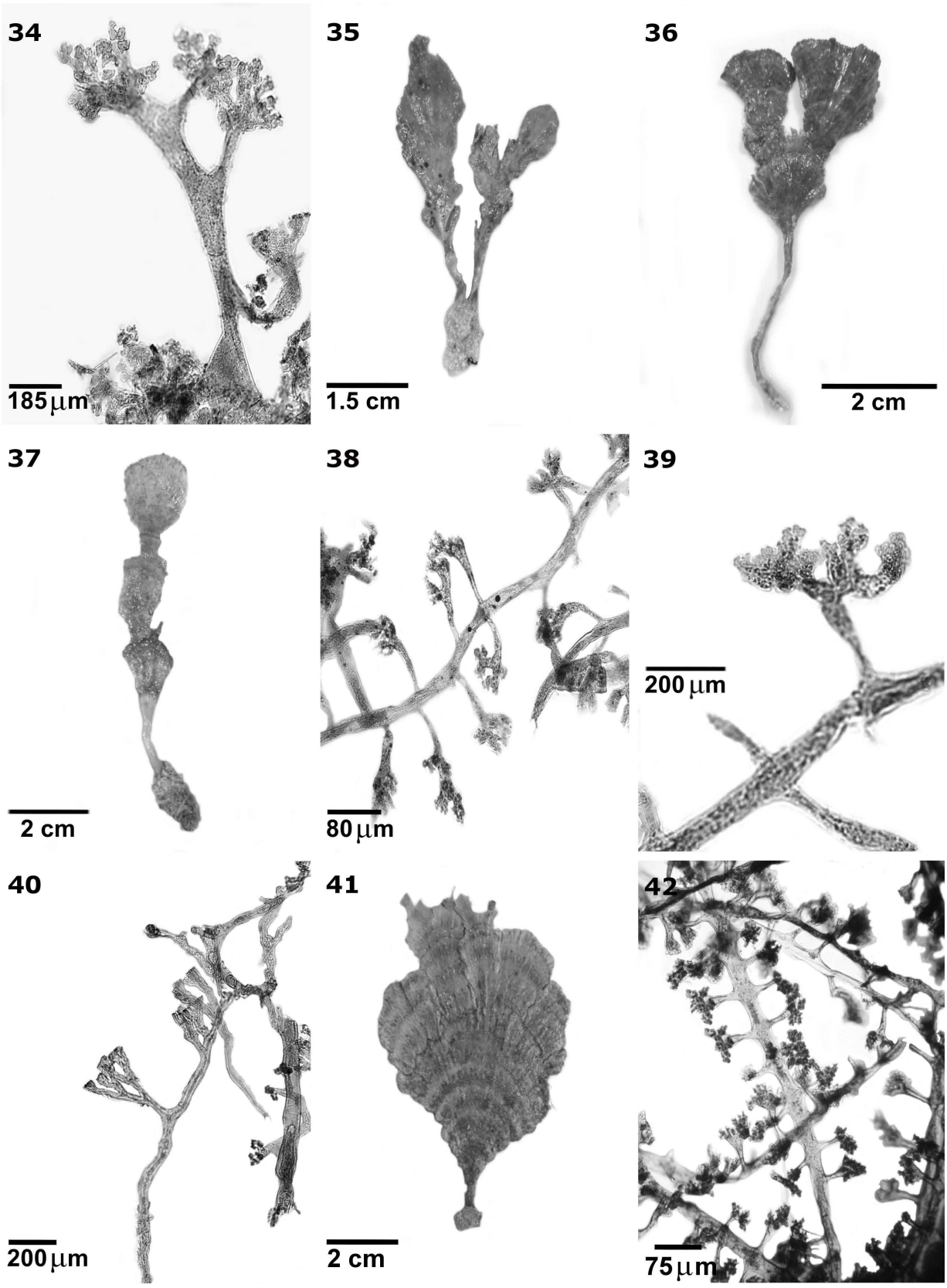
Comments:—Taylor (1928) described for the first time *Udotea sublittoralis* from specimens with the funnel-shaped lamina, not flattened with spongy appearance and with irregularly branched lateral appendages and folded or truncated apices. However, Littler & Littler (1990) considered that those specimens corresponding to *U. sublittoralis* should be considered as a form of the parental species (*U. cyathiformis*), thus, they assigned the name *U. cyathiformis* f. *sublittoralis* to those specimens of fibrous and cup-like appearance. In this work, the shape of the stipe appendages coincides with those described by Taylor (1928) and Littler & Littler (1990), however the blade shape was different from what these authors mention. The diameter of stipe and blade siphons does not match those registered by Taylor (1928) and Littler & Littler (1990). The presence of this taxon is confirmed in the Quintana Roo coast and it is a first-time record for Campeche shores.

Udotea cyathiformis var. ***flabellifolia*** D.S. Littler & M.M. Littler 1990: 220

Type locality:—PANAMA. San Blas Island.

Morphology:—Thalli to 8 cm tall, anchored on substrata by a bulbous rhizoidal mass. Stipe cylindrical 10–15 mm length, 2–5 mm diameter, and flattening towards the blade. Evident transition between the stipe and blade. Blade fan-shaped or orbicular, grass green, slightly wider (1.5–8 cm) than longer (1–6 cm), lower margin ovate o truncate, multistratose, ecorticate, lightly calcified, and clearly zonate (Figs. 31, 32).

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 45–55 µm in diameter, one of the siphons of the dichotomy gives rise to another dichotomy and the other continues to grow thus forming sub-dichotomies (Fig. 33). Distance between each dichotomy varies from 1300 to 2500 µm, supra dichotomous constrictions 19–27 µm length, 15–25 µm in diameter. Stipe siphons adjacent to lateral appendages 50–74 µm in diameter, appendages peduncle 70–250 µm length, 25–40 µm in diameter. Appendices arranged irregularly and dichotomously branched 2–3 times, with distorted digitate apices (Fig. 34).



FIGURES 34. *U. cyathiformis* var. *flabellifolia*. 34) stipe lateral appendages. **FIGURES 35–40**. *U. dixonii*. 35–37) external morphology, 38) blade siphon showing the opposite lateral appendages, 39) blade lateral appendages, 40) stipe lateral appendages. **FIGURES 41–42**. *U. dotyi*. 41) external morphology, 42) blade siphons showing the lateral appendages arrangement.

Reproduction:—Vegetative.

Material examined:—MEXICO. Quintana Roo, Santa Rosa, 9 September 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23110. MEXICO. Quintana Roo, Santa Rosa, 12 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23111. MEXICO. Quintana Roo, Punta Akumal, 16 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23112. MEXICO. Quintana Roo, Cayo Valencia, 16 August 2012, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 20887. MEXICO. Campeche, Playa Villamar, 25 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23109. MEXICO. Campeche, Payucán, 25 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23108. MEXICO. Campeche, Punta Xen, 20 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23107.

Geographic distribution:—Panama, Cuba, Brazil, Mexico.

Habitat:—Rocky in reef lagoons and sandy bottoms associated with sea grass meadows. Subtidal to 2 m depth.

Comments:—*Udotea cyathiformis* var. *flabellifolia* is distinguished by flabellate blade and the deformed stipe appendages in comparison with the cup shape of the parental specie (*U. cyathiformis*) and spatulate shape of the *sublittoralis* form. The shape of the stipe appendages agrees which those described by Littler & Littler (1990). Santos & Nunes (2014) provided detailed information about the morphology of this taxon and its occurrence in Brazil. This taxon has been recorded only in the Quintana Roo coast (Acosta-Calderón *et al*. 2016), thus, in this paper the distribution of *U. cyathiformis* var. *flabellifolia* is extended to the Quintana Roo coast and is recorded for the first time for the Campeche littoral.

Udotea dixonii D.S. Littler & M.M. Littler 1990: 220

Type Locality:—BELIZE, on the East side of Curlew Cay.

Morphology:—Thalli to 12 cm tall, anchored on substrata by a bulbous mass of entangled mass of fibrous rhizoids. It occurs as individuals or in groups of two to six thalli arising from the same rhizoidal mass. Stipe terete 6–37 mm long, 2–6 mm in diameter, transition between stipe and blade not evident. Spatulate blade 2–8 cm length, 1–10 cm wide, green in color, longer (3–7 cm) than wider (2–4 cm), lower margin ovate, multistratose, corticate, heavily calcified, and distinct concentric zones (Figs. 35, 36, 37).

Anatomy:—Blade siphons with lateral appendages, dichotomously branched, 22–40 µm in diameter, blade appendages arranged in two vertical rows (opposite) (Fig. 38), terminating in many, swollen knobs of short projection (Fig. 39), blade appendages peduncle 12–24 µm in diameter, 60–160 µm in length. Stipe siphons adjacent to lateral appendages 22–68 in diameter, appendages peduncle 140–525 µm length, 20–45 µm in diameter. Stipe appendages branched 2–3 times, with dichotomously divided, stubby, digitate projections, appendages (Fig. 40) intertwined and in such close proximity that it is difficult to separate components of the stipe cortex.

Reproduction:—The terminal portion of the fertile frond becomes loose, and as the filaments separate the sexual reproductive organs can be observed.

Material examined:—MEXICO. Quintana Roo, Uvero, 10 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23128. MEXICO. Quintana Roo, Punta Piedra, 17 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23124. MEXICO. Quintana Roo, Isla Mujeres, 16 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23123. MEXICO. Quintana Roo, Punta Akumal, 16 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23126. MEXICO. Quintana Roo, Isla Cozumel, 18 September 1993, R. Robles, ENCB 16650. MEXICO. Quintana Roo, Punta Pelicanos, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, 14 August 2012, ENCB 20818. MEXICO. Yucatan, Santa Clara Pueblo, 16 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23127. MEXICO. Campeche, Bahía Campeche, 24 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23125. MEXICO. Campeche, Payucán, 23 October 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23129. MEXICO. Campeche, Lerma, 23 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23131. MEXICO. Campeche, Playa Villamar, 26 October 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23130. MEXICO. Campeche, Champoton, 17 October 2004, ENCB 17287.

Geographic distribution:—Florida, Haiti, Puerto Rico, Flower Garden Banks, Belize, Nicaragua, Panama, Cuba, Brazil, Mexico.

Habitat:—Subtidal rocky platforms with soft waves and sandy bottom with sea grass meadows to 2 m depth.

Comments:—The internal structure of *U. dixonii* resembles that of *U. dotyi*, which also possesses numerous

blade appendages arranged opposite. However, whereas the blade appendages of *U. dotyi* terminate in a cluster of flattened tips, those of *U. dixonii* terminate in a dense array of short and swollen projection. Morphologically, *U. dixonii* resembles *U. flabellum*, although its blades are thinner, delicate, longer than wider, and the stipe is less wide. The dimensions of the blade and stipe siphons agree with those described by Littler & Littler (1990) and Collado-Vides *et al*. (2009).

Udotea dotyi D.S. Littler & M.M. Littler 1990: 223

Type Locality:—GRENADINES. Lesser Antilles, Tobago Cays.

Morphology:—Thalli to 11 cm tall, anchored to the substrata by a bulbous mass of rhizoids. Stipe flattened and robust, 8–13 mm length, 3–5 mm diameter, there is no differentiation between the stipe and blade. Blade fan-shaped, occasionally lobed, green, slightly longer (7–10 cm) than wider (6–7.5 cm), lower margin ovate or truncate, multistratose, corticate, heavily calcified, and faint concentric zonation (Fig. 41).

Anatomy:—Blade siphons with lateral appendages, 20–40 µm in diameter, densely covered by two opposite rows of short lateral appendages (Fig. 42) with irregular flat apices, blade appendages peduncle 15–30 µm in diameter, 60–120 µm length (Fig. 43). Stipe siphons adjacent to lateral appendages 40–70 µm in diameter, appendages peduncle 150–300 µm length, 20–40 µm in diameter. Appendages branched twice, terminating in numerous blunt rounded tips (Fig. 44).

Reproduction:—The terminal portions of the blade siphons are transformed into sexual reproductive organs named gametangia.

Material examined:—MEXICO. Quintana Roo, Uvero, 20 June 2010, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23133. MEXICO. Campeche, Xpicob, 25 June 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23132.

Geographic distribution:—Honduras, Panama, Cuba, Haiti, Lesser Antilles, Puerto Rico, Mexico.

Habitat:—Sandy bottom with sea grass. Subtidal to 3 m depth.

Comments:—*Udotea dotyi* can be confused with *U. flabellum* because both possess a corticated fan-shaped blade, but the arrangement and shape of the blade's lateral appendages are clearly different between these species. On the other hand, *U. dotyi* and *U. dixonii* possess blade siphons covered with two rows of lateral appendages, nevertheless the shape of the blade's lateral appendages is different. The shape of the blade and stipe appendages agrees with those described by Littler & Littler (1990). The diameter of blade and stipe siphons is less than those recorded in specimens from Haiti and Honduras (Littler & Littler 1990), buy are like those recorded in algae from Quintana Roo, Mexico (Collado-Vides *et al*. 2009). *Udotea dotyi* was an uncommon species in the study area and is recorded for the first time for the Campeche littoral.

Udotea fibrosa D.S. Littler & M.M. Littler 1990: 226

Type locality:—BELIZE. Carrie Bow Cay.

Morphology:—Thalli to 6.5 cm tall, anchored on substrata by a bulbous mass of entangled rhizoidal siphons. Stipe cylindrical 6–12 mm long, 2–4 mm in diameter. Evident transition between the stipe and blade. Blade spatulate, green, longer (4–5 cm) than wider (1–1.5 cm), lower margin oval, multistratose, ecorticate (no lateral appendages), calcified, and not zonate (Figs. 45, 46).

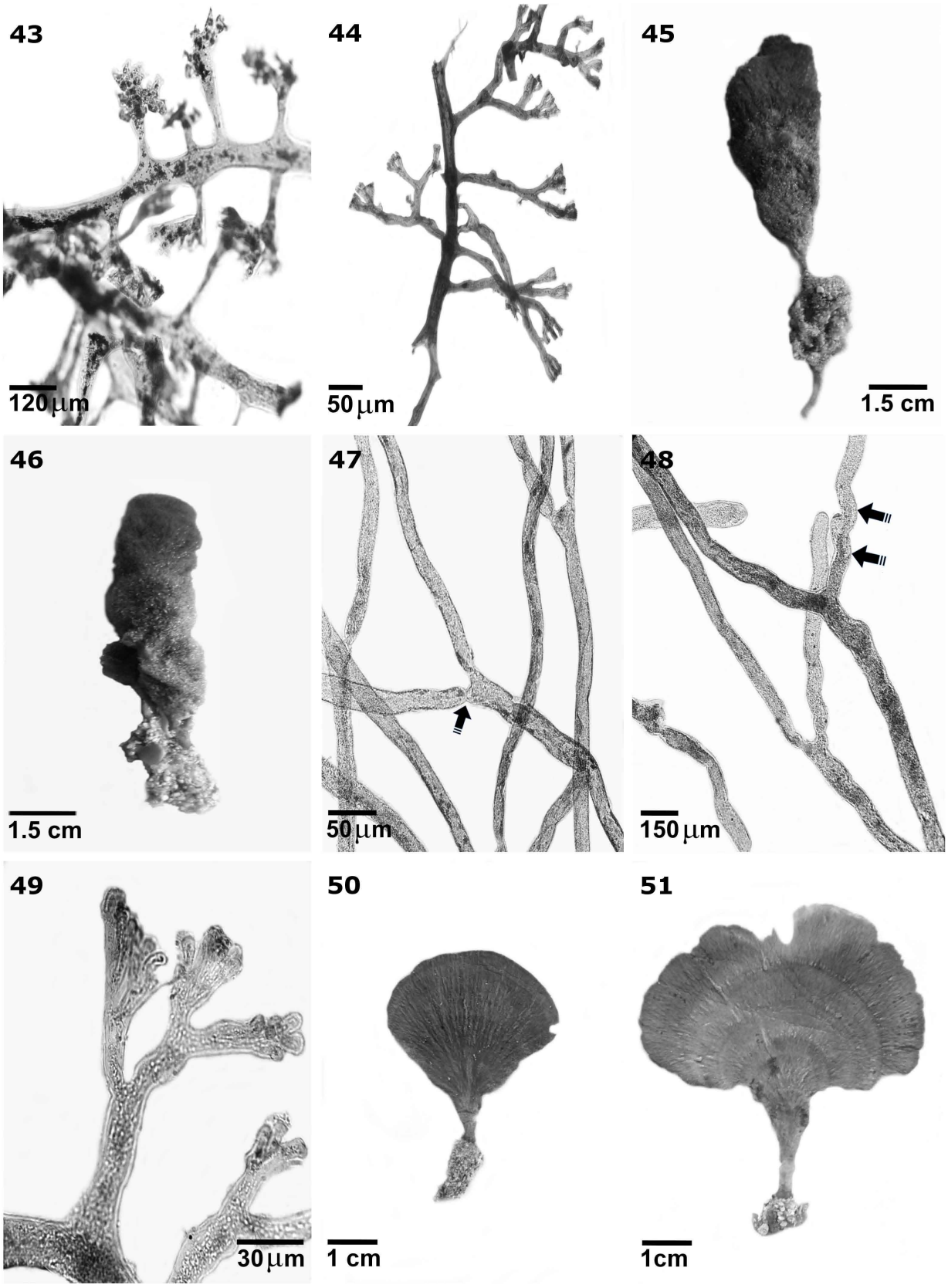
Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 50–70 µm in diameter, supradichotomic constrictions 15–17 µm length, 18–23 µm in diameter (Fig. 47), some blade siphons torulose (Fig. 48). Stipe siphons adjacent to lateral appendages 27–47 µm in diameter, appendages peduncle 90–150 µm length, 20–30 µm in diameter. Appendages dichotomously branched 2–3 times, with swollen dichotomously tips (Fig. 49).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Isla Mujeres, 16 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23136. MEXICO. Quintana Roo, Punta Placer, 13 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23135. MEXICO. Quintana Roo, Santa Rosa, 12 April 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23134.

Geographic distribution:—Belize, Cuba, Haiti, Jamaica, Martinique, Mexico.

Habitat:—Rocky platforms with moderate surge and fresh water influence from mangroves. Subtidal to 1 m depth.



FIGURES 43–44. *U. dotyi*. 43) blade lateral appendages, 44) stipe lateral appendages. **FIGURES 45–49.** *U. fibrosa*. 45–46) external morphology, 47) blade siphons, 48) detail of the supradichotomic constriction of the blade siphon, 49) stipe lateral appendages. **FIGURES 50–51.** *U. flabellum*. 50–51) external morphology.

Comments:—*Udotea fibrosa* differs from the other species by the absence of lateral appendices in the siphons of the spatulate blade, lack of zonation, fibrous texture and shape of the stipe appendages. The diameters of stipe and blade siphons are smaller than those reported in specimens from Belize (Littler & Littler 1990), Punta Brava, Quintana Roo, Mexico (Collado-Vides *et al*. 2009) and Cuba (Moreira *et al*. 2013). Littler & Littler (1990) mention that *U. fibrosa* has wider blade siphons than *U. conglutinata* and *U. abbottiorum*. In this study, the diameter of blade siphons between *U. fibrosa* and *U. abbottiorum* were relatively similar. *Udotea fibrosa* can be confused with *U. cyathiformis* f. *sublittoralis* since both have a coarse fibrous texture and spatulate blade, however, the blade of *U. fibrosa* lacks the zonation bands characteristically shown by *U. cyathiformis* f. *sublittoralis.* This species was uncommon in the study area and has been registered only for Puerto Morelos (Collado-Vides *et al*. 2009), and Punta Xoquen in the Biosphere Reserve of Sian Ka'an, Mexico (Acosta-Calderón *et al*. 2016).

Udotea flabellum (J. Ellis & Solander) M.A. Howe 1904: 94

Basionym:—*Corallina flabellum* J. Ellis & Solander 1786

Heterotypic Synonyms**:**—*Udotea flabellata* J.V. Lamouroux 1816

Type Locality:—WEST INDIES.

Morphology:—Thalli to 10 cm tall, anchored on substrata by a bulbous to elongated mass of fibrous rhizoids. Stipe cylindrical, short and robust or thin, flattening toward the blade, 5–47 mm length, 3–6 mm diameter. Transition between the stipe and blade is not evident. Blade fan-shaped with many overlapping lobes, dark green, almost wider (2.5–10 cm) than longer (2–8.7 cm), lower margin ovate or truncate, multistratose, ecorticate, heavily calcified, and marked by distinct concentric zonation lines (Figs. 50–53).

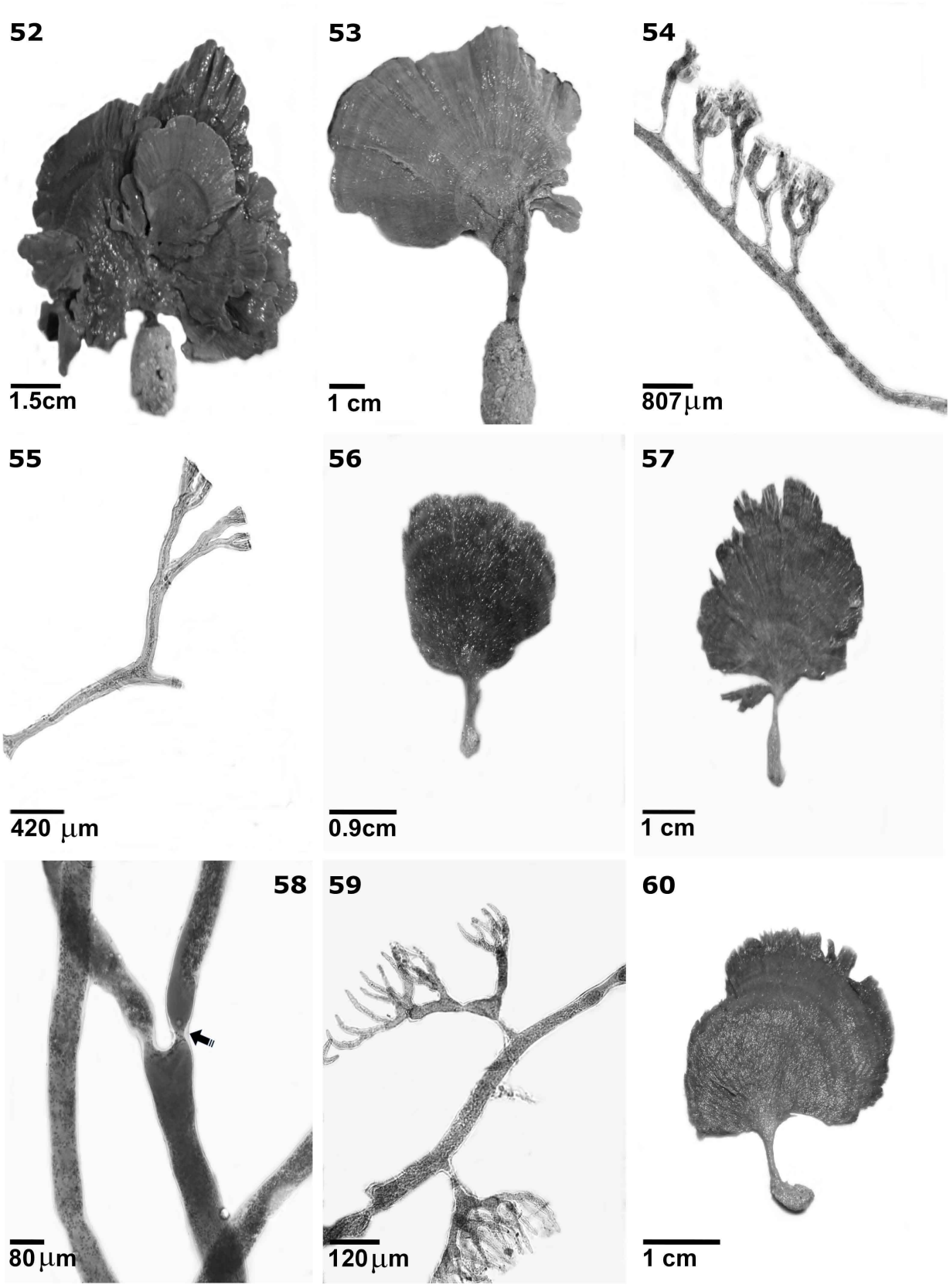
Anatomy:—Blade siphons with lateral appendages, dichotomously branched, 20–30 µm in diameter, blade appendages arranged irregularly spaced long-stemmed, terminating in many, short, dichotomously branched projections, apices swollen and flat (Fig. 54), blade appendages peduncle 12–21 µm in diameter, 60–150 µm in length. Stipe siphons adjacent to lateral appendages 27–60 in diameter, peduncle 120–480 µm length, 25–45 µm in diameter. Appendages branched twice, with dichotomously small tips (Fig. 55).

Reproduction:—The terminal portion of the fertile frond becomes loose, and as the filaments separate the reproductive structure can be observed.

Material examined:—MEXICO. Quintana Roo, Santa Rosa, 11 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23146. MEXICO. Quintana Roo, Uvero, 10 June 2014, J.A. Acosta Calderón, Mateo Cid, A.C. Mendoza González, ENCB 23139. MEXICO. Quintana Roo, Punta Rio Bermejo, 12 April 2015, J.A. Acosta Calderón, Mateo Cid, A.C. Mendoza González, ENCB 23145. MEXICO. Quintana Roo, Rio Indio, 11 September 2014, J.A. Acosta Calderón, Mateo Cid, A.C. Mendoza González, ENCB 23138. MEXICO. Quintana Roo, Punta Akumal, 16 December 2014, J.A. Acosta Calderón, L.E. L.E. Mateo Cid, A.C. Mendoza-González, ENCB 23147. MEXICO. Quintana Roo, Akumal, 24 December 2002, L. Huerta Múzquiz, A.C. Mendoza González, ENCB 16177. MEXICO. Yucatán, Santa Clara Pueblo, 20 June 2011, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza-González, ENCB 23140. MEXICO. Yucatán, Progreso, 15 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza-González, ENCB 23141. MEXICO. Yucatán, Ria Lagartos, 22 November 1997, L. Huerta Múzquiz, I. Sánchez Molina, R. Rojas, ENCB 13494. MEXICO. Yucatán, San Crisanto, 23 June 2006, L.E. Mateo Cid, A.C. Mendoza González, ENCB 18501. MEXICO. Campeche, Punta Xen, 26 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza-González, ENCB 23144. MEXICO. Campeche, Xpicob, 25 June 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza-González, ENCB 23143. MEXICO. Campeche, La Ensenada, 27 June 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza-González, ENCB 23137. MEXICO. Campeche, Puerto Real, 26 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza-González, ENCB 23142. MEXICO. Campeche, 26 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23142. MEXICO. Campeche, Playa Bonita, 19 April 2007, L.E. Mateo Cid, A.C. Mendoza González, ENCB 22811.

Geographic distribution:—Bermuda, Florida, Belize, North Carolina, Texas, Panama, Bahamas, Caiman Island, Cuba, Jamaica, Lesser Antilles, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela, Kenya, Somalia, Tanzania, India, Sri Lanka, China, Indonesia, Malaysia, Philippines, Tailand, Vietnam, New Zealand, Mexico.

Habitat:—Rocky platforms with soft waves, sandy bottom with sea grass meadows, reef lagoons. Subtidal to 5 m depth.



FIGURES 52–55. *U. flabellum*. 52–53) external morphology, 54) blade lateral appendages, 55) stipe lateral appendages. **FIGURES 56–59.** *U. looensis*. 56–57) external morphology, 58) detail of the supradichotomic constriction of the blade siphon, 59) stipe lateral appendage. **FIGURES 60**. *U. luna.* 60) external morphology.

Comments:—The first morphological description of this species was made by J. Ellis & Solander (1786), as *Corallina flabellum*. Later, Lamouroux (1816) made the change from *C. flabellum* to *Udotea flabellata*. Howe (1904) made the combination *Udotea flabellum.* Taylor (1960) provided information about the morphology of *U. flabellum* thalli. Finally, Littler & Littler (1900) provided a detailed description of the morphological and anatomical characters used in the species segregation in this genus. In this study, *U. flabellum* may have a short and wide stipe or cylindrical, flattening toward the blade, however the shapes of the blade and stipe appendages are constant characters. This species can be confused with *U. dotyi*, *U. dixonii*, *U. norrisii,* and *U. occidentalis* by the blade morphology; however, the internal structure separates these five species. The shape of the blade and stipe appendages agrees with those described by Taylor (1960) and Littler & Littler (1990). Nevertheless, the diameter of blade siphons is less than those recorded in specimens from Florida, USA (Littler & Littler 1990). But similar than those record from Quintana Roo, Mexico (Collado-Vides *et al*. 2009). It is the most widespread species of *Udotea* in the Yucatan peninsula littoral.

Udotea looensis D.S. Littler & M.M. Littler: 1990: 232

Type Locality:—USA, Looe Key, Monroe County, Florida.

Morphology:—Thalli to 5 cm tall, anchored on substrata by a small bulbous mass of entangled rhizoidal siphons. Stipe cylindrical 3–6 mm long, 1–3 mm in diameter, evident transition between the stipe and blade. Blade orbicular or reniform, green, as long (1–4.5 cm) as wide (1–4.7 cm), lower margin oval o reniform, multistratose with unistratose outer margin, ecorticate (no lateral appendages), slightly calcified, and clearly zonate (Figs. 56, 57).

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 35–55 µm in diameter, distance between each dichotomy varies from 700 to 1600 µm, supra dichotomous constrictions 30–40 µm length, 12–24 µm in diameter (Fig. 58). Stipe siphons adjacent to lateral appendages 40–60 µm in diameter, appendages peduncle 60–120 µm length, 20–40 µm in diameter. Appendages dichotomously branched 1–2 times, with abundant dichotomously lanceolate and apiculate apices (Fig. 59).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Punta Mahahual, 10 September 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23152. MEXICO. Quintana Roo, Punta Akumal, 16 December 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23151. MEXICO. Quintana Roo, Rio Indio, 13 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23154. MEXICO. Quintana Roo, El Zarzal, 19 May 1998, R.B. Searles, ENCB 17513. MEXICO. Quintana Roo, Faro de Bahía Espíritu Santo, 21 March 2009, J.A. Acosta Calderón, ENCB 20045. MEXICO. Yucatán, Progreso, 20 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23153. MEXICO. Campeche, Playa Villamar, 25 January 2016, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23150. MEXICO. Campeche, Punta Xen, 20 June 2014, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23149. MEXICO. Campeche, Payucán, 27 October 2015, J.A. Acosta Calderón, L.E. Mateo Cid, A.C. Mendoza González, ENCB 23148. MEXICO. Campeche, Lerma, 19 September 1965, A. Vargas, ENCB 16732.

Geographic distribution:—Florida, Belize, Honduras, Panama, Bahamas, Cuba, Martinique, Mexico.

Habitat:—Rocky platforms with moderate surge and calcareous rocks in turbid waters. Subtidal to 5 m depth.

Comments:—Littler & Littler (1990) indicate that *Udotea looensis* shows morphologically similitudes to *U. luna* and *U. spinulosa*, however in this study morphological differences were found in the blade shape between them; for example *U. looensis* does not present lateral appendages in blade siphons like *U. spinulosa*, besides *U. looensis* differs from the other species by the lateral appendages' shape. The diameter of blade siphons is smaller than those recorded in specimens from Florida (Littler & Littler 1990), but similar to those documented in specimens from Puerto Morelos, Quintana Roo, Mexico (Collado-Vides *et al*. 2009). This species has been recorded only for one site in Campeche (Mateo-Cid *et al.* 2013), but in in this paper the distribution of this species extended along the Campeche coast and is recorded for the first time for the Yucatan shore.

Udotea luna D.S. Littler & M.M. Littler 1990: 232

Type locality:—USA. Florida**,** Content Keys, Monroe County.

Morphology:**—**Thalli to 5 cm tall, anchored on substrata by a small bulbous mass of entangled rhizoidal siphons. Stipe cylindrical 4–9 mm long, 2–6 mm in diameter, gradual transition between the stipe and blade. Blade orbicular or reniform, green, slightly wider (1.7–4.5 cm) than longer (1.4–3 cm), lower margin oval o reniform, multistratose, ecorticate (no lateral appendages), slightly calcified, and clearly zonate (Figs. 60, 61).

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 35–55 µm in diameter (Fig. 62), distance between each dichotomy varies from 900 to 1600 µm, supra dichotomous constrictions 25–40 µm length, 9–15 µm in diameter (Fig. 63). Stipe siphons adjacent to lateral appendages 33–63 µm in diameter, appendages peduncle 20–120 µm length, 10–45 µm in diameter. Appendages dichotomously branched 1–2 times, with wide dichotomously acute and lanceolate apices (Fig. 64).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Punta Akumal, 16 December 2014, A.C. Mendoza-González, L.E. Mateo Cid, J.A. Acosta Calderón, ENCB 23163. MEXICO. Quintana Roo, Puerto Morelos, 15 June 2014, A.C. Mendoza-González, L.E. Mateo Cid, J.A. Acosta Calderón, ENCB 23160. MEXICO. Quintana Roo, Pulticub, 14 April 2015, A.C. Mendoza-González, L.E. Mateo Cid, J.A. Acosta Calderón, ENCB 23162. MEXICO. Quintana Roo, Rio Indio, 19 December 2014, A.C. Mendoza-González, L.E. Mateo Cid, J.A. Acosta Calderón, ENCB 23161. MEXICO. MEXICO. Quintana Roo, Faro Bahía Espíritu Santo, 21 March 2009, J.A. Acosta Calderón, ENCB 20001. MEXICO. Campeche, Payucán, 25 October 2015, A.C. Mendoza-González, L.E. Mateo Cid, J.A. Acosta Calderón, ENCB 23158. MEXICO. Campeche, Punta Xen, 20 June 2014, A.C. Mendoza-González, L.E. Mateo Cid, J.A. Acosta Calderón, ENCB 23157. MEXICO. Campeche, Punta Xen, 14 October 2004, A.C. Mendoza-González, L.E. Mateo Cid, ENCB 17825. MEXICO. Campeche, Playa Villamar, 25 January 2016, A.C. Mendoza-González, L.E. Mateo Cid, J.A. Acosta Calderón, ENCB 23155.

Geographic distribution:—Bahamas, Florida, Belize, Cuba, Mexico.

Habitat:—Rocky platforms with soft waves and calcareous rocks in turbid waters. Subtidal to 2 m depth.

Comments:—Littler & Littler (1990) indicate that *U. luna* shows morphologically similitude to *U. looensis*, nevertheless in this study morphological differences were found in the blade shape between them; *U. luna* has an oval blade with lower margin truncated or reniform, whereas *U. looensis* shows an orbicular blade with lower oval margin. In addition, the superior margin of the blade is unistratose in *U. looensis*, whereas *U. luna* presents a multistratose superior margin, as mentioned by Littler & Littler (1990). The diameter of stipe and blade siphons are smaller than those recorded in specimens from Belize (Littler & Littler 1990), but similar to those documented in specimens from Puerto Morelos, Quintana Roo, Mexico (Collado-Vides *et al*. 2009). Finally, this species is recorded for the first time for the Campeche shore.

Udotea norrisii D.S. Littler & M.M. Littler 1990: 235

Type Locality:—BAHAMAS. Chub Cay, Andros Reef.

Morphology:—Thalli to 8.5 cm tall, anchored on substrata by a bulbous mass of entangled rhizoidal siphons. Stipe cylindrical, heavy calcified, 6–15 mm long, 3–6 mm in diameter, transition between the stipe and blade is not evident. Blade flabellate o spatulate, green, the blade can be as long as wide or longer than wider, with longitudinal proliferations, lower margin ovate o truncate, multistratose, corticated (with lateral appendages), heavily calcified, and clearly zonate (Fig. 65, 66).

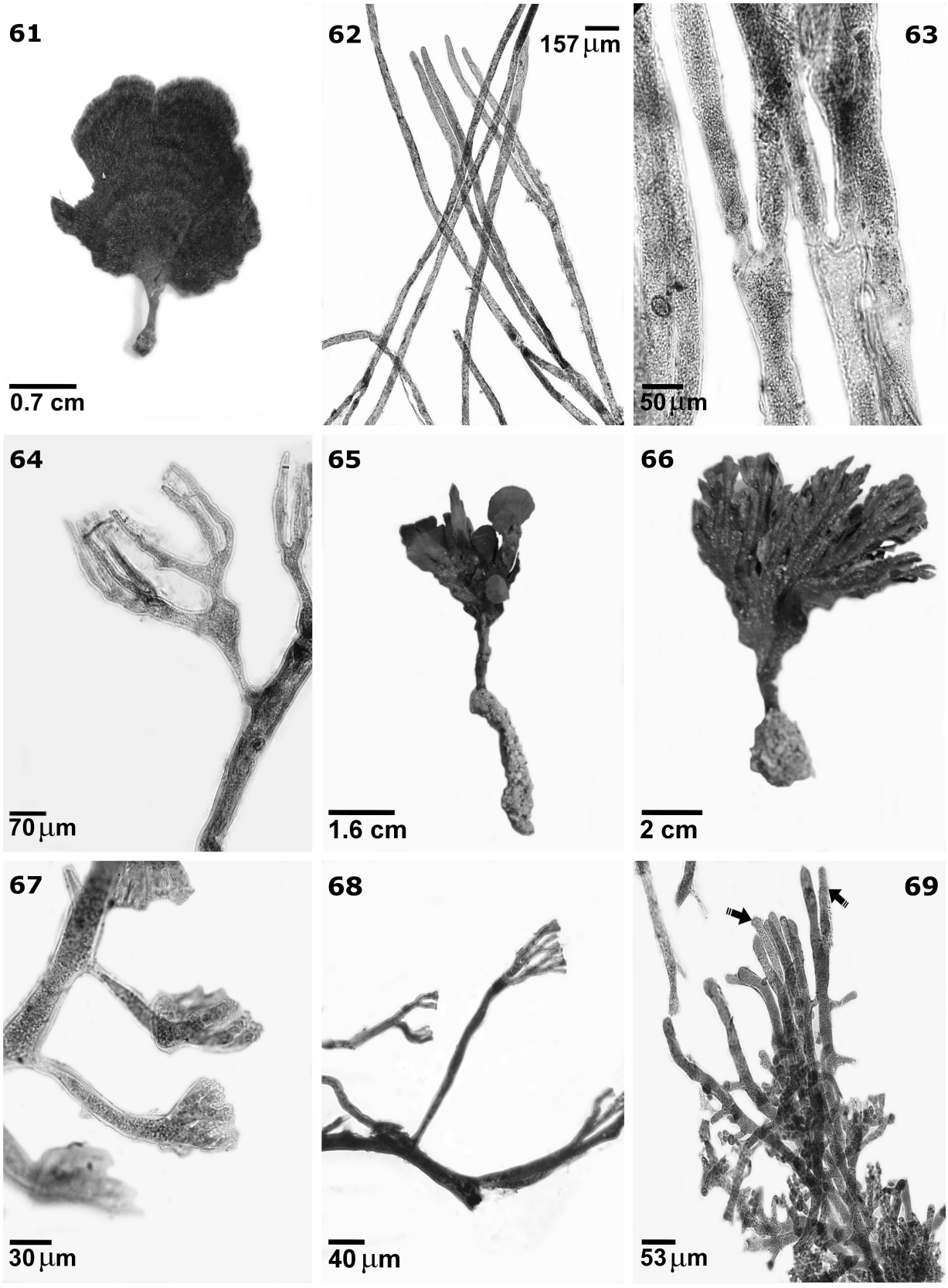
Anatomy:—Blade siphons with lateral appendages, dichotomously branched, 20–30 µm in diameter, siphons possess wide and irregularly spaced lateral appendages(Fig. 67), tightly adherent at the tips, appendages peduncle 90–120 µm length, 13–18 µm in diameter, with short swollen and flat dichotomously apices. Stipe siphons adjacent to lateral appendages 25–45 µm in diameter, appendages peduncle 100–160 µm length, 19–25 µm in diameter, appendages dichotomously branched 1–2 times, with swollen tips (Fig. 68).

Reproduction:—An indication of the presence of sexual reproductive structures is the development of a darkened region in the distal portion of the blade, these structures are tubular extensions of the siphons (Fig. 69).

Material examined:—MEXICO. Quintana Roo. Punta Rio Bermejo, 12 April 2015, J.A. Acosta-Calderón, L.E. Mateo-Cid, A.C. Mendoza-González, ENCB 23177. MEXICO. Quintana Roo, Punta Akumal, 16 December 2014, J.A. Acosta-Calderón, L.E. Mateo-Cid, A.C. Mendoza-González, ENCB 23175. MEXICO. Quintana Roo, Santa Rosa, 12 April 2015, J.A. Acosta-Calderón, L.E. Mateo-Cid, A.C. Mendoza-González, ENCB 23174. MEXICO. Campeche, Payucán, 23 October 2015, J.A. Acosta-Calderón, L.E. Mateo-Cid, A.C. Mendoza-González, ENCB 23176. MEXICO. Campeche, La Ensenada, 27 June 2016, J.A. Acosta-Calderón, L.E. Mateo-Cid, A.C. Mendoza-González, ENCB 23178.

Geographic distribution:—Bermuda, Bahamas, Cuba, Mexico.

Habitat:—Rocky and sandy bottoms with moderate surge. Subtidal to 2 m depth.



FIGURES 61–64. *U. luna*. 61) external morphology, 62) blade lateral appendages, 63) detail of the supradichotomic constriction of the blade siphon, 64) stipe lateral appendage. **FIGURES 65–69.** *U. norrisii*. 65-66) external morphology, 67) blade lateral appendages, 68) stipe lateral appendage, 69) detail of the upper portion of the blade siphon showing sexual reproductive structures.

Comments:—According to Littler & Littler (1990), the internal anatomy of *U. norrisii* is similar to *U. flabellum*, however in this study, marked differences were observed between the shape of the blade and stipe appendages. These authors also mention that *U. norrisii* has a longitudinal divided blade, but the specimens of *U. norrisii* found in the study area presented a flabellate blade, so that the characters useful to determine this species were the shape of stipe and blade appendages. *Udotea norrisii* is registered for the first time for the Quintana Roo and Campeche littoral.

Udotea occidentalis A. Gepp & E.S. Gepp 1911: 127

Type locality:—USA. St. Thomas, Virgin Islands.

Morphology:—Thalli to 5 cm, anchored on soft substrata by a bulbous mass of rhizoids. Stipe cylindrical, robust, 8–10 mm length, 5–6 mm diameter, there is no differentiation between stipe and blade. Blade fan-shaped, multilobed, light green, wider (7–8 cm) than long (4–5 cm, lower margin is reniform, multistratose, corticated, heavily calcified, and fain concentric zonation (Fig. 70).

Anatomy:—Blade siphons with lateral appendages, 30–40 µm in diameter, densely covered by two opposite rows of short lateral appendages (Fig. 71), possessing 8–15 low unique knobs with appearances of sunken blade appendages, peduncle 10–20 µm in diameter, 40–65 µm length (Fig. 72). Stipe siphons adjacent to lateral appendages 30–60 µm in diameter, appendages peduncle 150–300 µm length, 20–30 µm in diameter. Appendages branched twice terminating in numerous rounded projections (Fig. 73).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Chankanab, Isla Cozumel, 15 May 1993, R.B. Searles, M. Volovseck, ENCB 12766

Geographic distribution:—Bermuda, Florida, Belize, Bahamas, Cuba, Puerto Rico, Virgin Islands, Brazil, Philippines, Mexico

Habitat:—Sandy bottom, subtidal to 12–15 m depth

Comments:—Gepp & Gepp (1911) described for the first time *Udotea occidentalis* based in morphological and anatomical character record from West Indies specimens. Littler & Littler (1990) mention that *U. occidentalis* can be confused with *Udotea flabellum* by the corticate blade; however both species can be differentiated by the presence of the fan-shape blade with a lower margin cordate and the uniquely lobed blade appendages. This species has been reported in depths greater than 5 m (Geep & Geep 1911, Littler & Littler 1990). This species was not located by the collections carried out in this study; hence, specimens from the ENCB herbarium were consulted to corroborate the record in the Yucatan peninsula littoral.

Udotea spinulosa M.A. Howe 1909: 97

Type locality:—BAHAMAS. Bimini Harbor.

Morphology:—Thalli delicate to 4 cm tall, anchored on substrata by a small bulbous mass of entangled rhizoidal siphons. Stipe cylindrical, slightly calcified, 4–6 mm long, 0.5 mm in diameter. Gradual transition between the stipe and blade. Blade flabellate or spatulate, green, longer (2–2.5 cm) than wider (1.5–2 cm), lower margin obtuse, multistratose in most part of the blade and unistratose in the superior margin, corticated (with lateral appendages), calcified, and slightly zonate (Fig. 74).

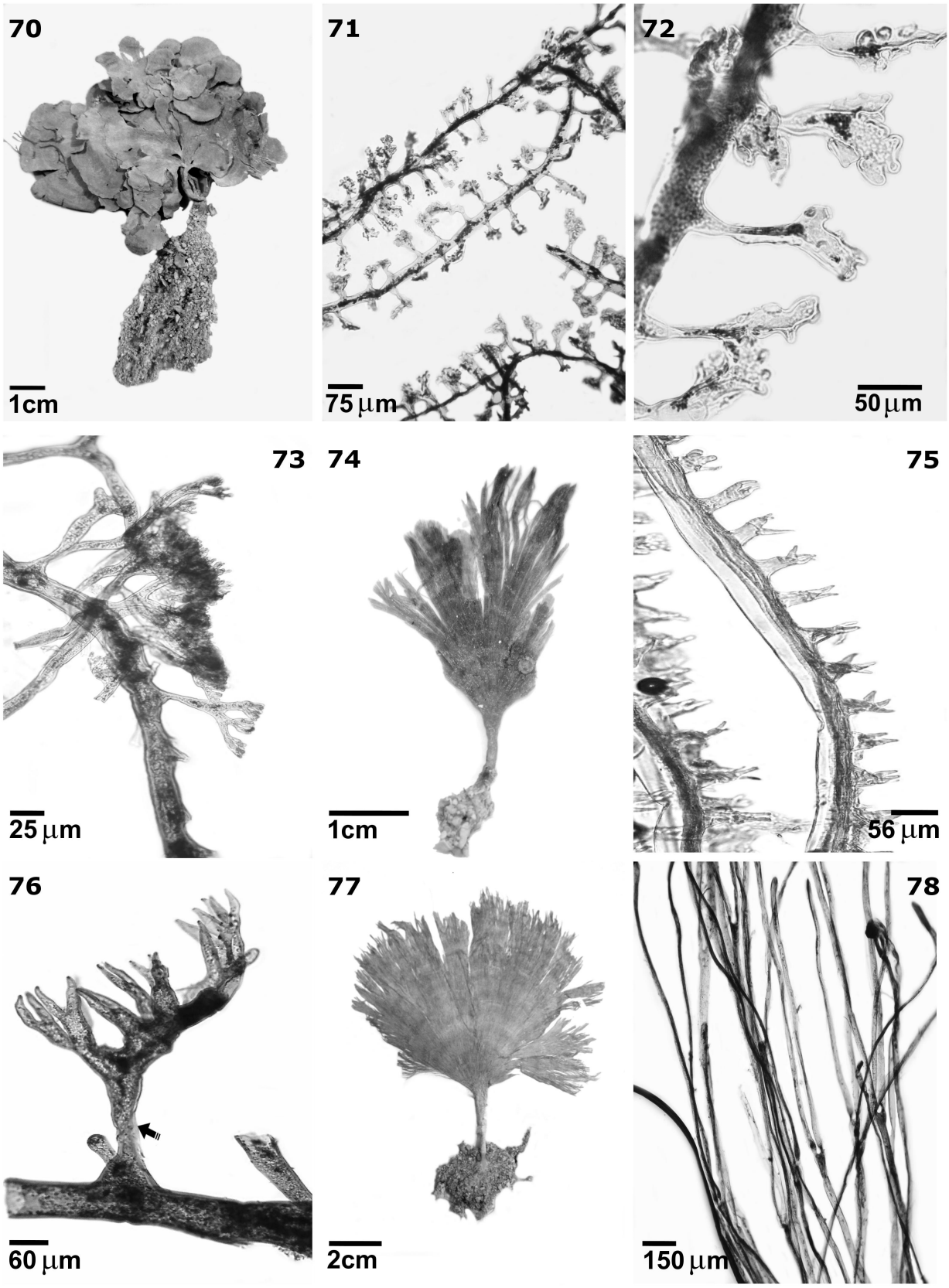
Anatomy:—Blade siphons with lateral appendages except in unistratose margin, dichotomously branched, 30–45 µm in diameter, distance between each dichotomy varies from 1500 to 1600 µm. From each dichotomy, one of the siphons branches dichotomically and the other continues to grow without branching. Blade appendages have a short peduncle from which 1–8 spine-like projections arise (Fig. 75). Stipe siphons adjacent to lateral appendages 45–60 µm in diameter, appendages peduncle 40–80 µm length, 20–25 µm in diameter. Appendages dichotomously branched once, with long, acute, digitate projections (Fig. 76).

Reproduction:—Vegetative

Material examined:—MEXICO. Yucatan, Progreso, 20 June 2014, J.A. Acosta-Calderón, L.E. Mateo Cid, A.C. Mendoza González. ENCB 23179. MEXICO. Campeche, Playa Villamar, 25 January 2016, J.A. Acosta-Calderón, L.E. Mateo Cid, A.C. Mendoza González. ENCB 23182. MEXICO. Campeche, Don Lin, 22-06-2004, P. López, ENCB 16999.

Geographic distribution:—Florida, Bahamas, Jamaica, Puerto Rico, Virgin Island, Seychelles, Mexico.

Habitat:—Rocky bottom, subtidal to 5 m deep.



FIGURES 70–73. *U. occidentalis*. 70) external morphology, 71) blade siphons showing the lateral appendages arrangement, 72) blade lateral appendages, 73) stipe lateral appendage. **FIGURES 74–76.** *U. spinulosa*. 74) external morphology, 75) blade lateral appendages, 76) stipe lateral appendage. **FIGURES 77–78.** *U. unistratea*. 77) external morphology, 78) blade siphons.

Comments:—Howe (1909) provide the first detail description of *Udotea spinulosa* based in morphological and anatomical characters of the blade and stipe. The shape of the stipe appendages agrees with those registered by Howe (1909), and Littler & Littler (1990). However, the diameter of siphons stipe and blade are smaller than those documented in specimens from Bahamas (Howe 1909), Jamaica, Puerto Rico (Littler & Littler 1990), and Cuba (Collado-Vides *et al*. 2009). *U. spinulosa* has been cited for several localities from Quintana Roo, Campeche, and Yucatan shores, however in this study few specimens were found only in Progreso, Yucatan, and Playa Villamar, Campeche.

Udotea unistratea D.S. Littler & M.M. Littler 1990: 240

Type Locality:—BELIZE. On the east side of Carrie Bow Cay.

Morphology:—Thalli to 9 cm tall, anchored to the substrata by a small compact mass of rhizoids siphons. Stipe cylindrical, 6–18 mm length, 3–4 mm wide. There is an evident transition between stipe and blade. Blade fan-shaped flat, delicate, longer (2–7.5 cm) than wider (2.5–9 cm), light green, lower margin acute, unistratose, ecorticate, slightly calcified and faint concentric lines present (Fig. 77).

Anatomy:—Blade siphons without lateral appendages, dichotomously branched, 30–60 µm in diameter (Fig. 78), distance between each dichotomy varies from 2000 to 8000 µm, supradichotomic constrictions 20–30 µm length, 20–25 µm in diameter (Fig. 79). Stipe siphons adjacent to lateral appendages 50–80 µm in diameter, appendages peduncle 120–300 µm length, 30–40 µm in diameter. Appendages dichotomously branched twice, constriction at the base and terminating in short dichotomously lobed, blunt tips (Fig. 80).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Chankanab, Isla Cozumel, 15 May 1993, R.B. Searles, M. Volovseck, ENCB 12797. MEXICO. Campeche, Don Lin, 22 June 2004. P. López, ENCB 19107.

Geographic distribution:—Florida, Belize, Bahamas, Cuba, Jamaica, Puerto Rico, Virgins Islands, Mexico

Habitat:—Sandy bottom, subtidal to 7–15 m depth.

Comments:—Blade characteristics and the shape of stipe lateral appendages of reviewed specimens correspond to those described for *Udotea unistratea* by Littler & Littler (1990). The diameter of blade and stipe siphons is less than those recorded in specimens from Bahamas, Jamaica, Belize (Littler & Littler 1990), Isla Cozumel (Collado-Vides *et al.* 2009) and Puerto Rico (Ballantine *et al*. 2011). *Udotea unistratea* can closely resemble the morphology of *Udotea cyathiformis* but is clearly distinguished by the unistratose blade and the shape of stipe appendages. Apparently, this species is distributed in the coast of Campeche and Quintana Roo at depths greater than 7 m. Littler & Litler (1990) reported that this specie occurs in deep water (to 46 m). Recently Ballantine *et al*. (2011) record *U. unistratea* to 70 m of deep.

Udotea wilsonii A. Gepp, E.S. Gepp & M.A. Howe 1911: 130–131, 144–145

Synonym:—*Geppina wilsonii* (A. Gepp, E. Gepp & M.A. Howe) Farghaly 1980

Type Locality:—BAHAMAS. North End, Salt Key Bank, Anguilla Isles.

Morphology:—Thalli to 5.5 cm tall, anchored on substrata by a compact rhizoidal mass. Stipe delicate, cylindrical 10 mm length, 2 mm diameter. Gradual transition between the stipe and blade. Blade flabellate, orbicular often lobed, green, as long (3.5–4.5 cm) as wide (4.5–4.8 cm), lower margin ovate or reniform, multistratose with the superior margin unistratose, corticate, calcified, zonation only visible backlit (Fig. 81).

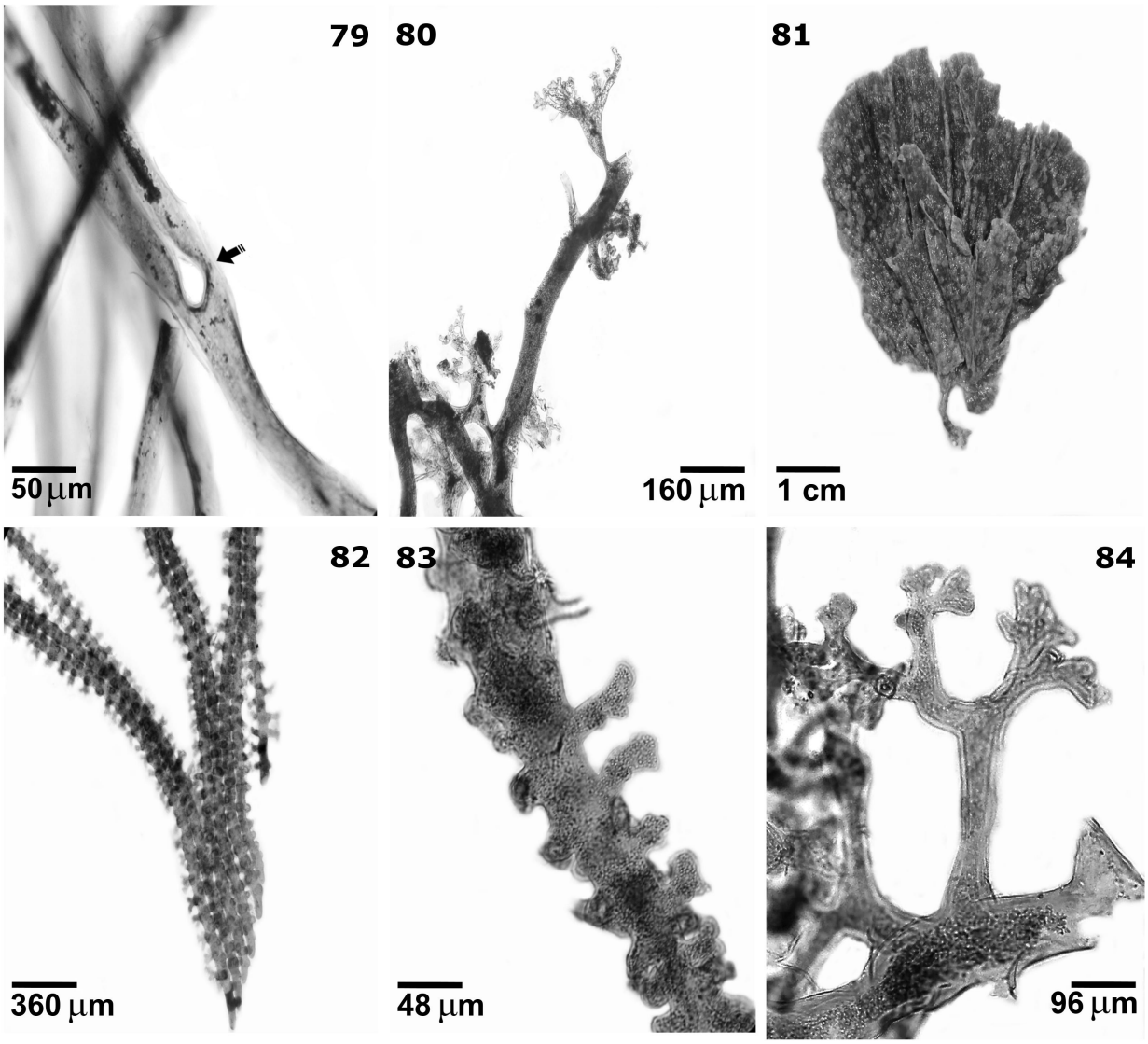
Anatomy:—Blade siphons with lateral appendages, dichotomously branched, 43–45 µm in diameter (Fig. 82), lacking supradichotomic constrictions, blade appendages short and knobby, simple or forked, 19–25 µm in diameter, in two to four vertical rows (Fig. 83). Stipe siphons adjacent to lateral appendages 45–60 µm in diameter, appendages peduncle 120–160 µm length, 20–25 µm in diameter. Appendages branched 2–3 times, with short swollen and flattened dichotomous tips (Fig. 84).

Reproduction:—Vegetative

Material examined:—MEXICO. Quintana Roo, Punta Akumal, 12 September 2014, L.E. Mateo-Cid, A.C. Mendoza-González, J.A. Acosta Calderón, ENCB 23180. MEXICO. Quintana Roo, Puerto Morelos, 20 March 1994. ENCB 18968. MEXICO. Quintana Roo, J.A. Acosta Calderón, Cocalito, Bahía Ascensión, ENCB 20002.

Geographic distribution:—Bermuda, Florida, Belize, Panama, Bahamas, Jamaica, Lesser Antilles, Mozambique, Mexico.

Habitat:—Rocky bottom associated to coral reefs, protected in cavities. Subtidal to 1 m depth.



FIGURES 79–80. *U. unistratea*. 79) detail of the supradichotomic constriction 80) stipe lateral appendage. **FIGURES 81–84.** *U. wilsonii*. 81) external morphology, 82) upper portion of the blade siphons, 83) blade lateral appendages, 84) stipe lateral appendages.

Comments:—Gepp & Gepp (1911) provide the first detail description of *Udotea wilsonii* based in morphological and anatomical characters of the blade and stipe. Specimens examined are broadly in line with the description of Gepp & Gepp (1911) and Littler & Littler (1990). However, the diameters of siphons stipe and blade are smaller than those recorded in specimens from Belize and Panama (Littler & Littler 1990) but similar than those mentioned by Gepp & Gepp (1911) and Collado-Vides *et al.* (2009). In this paper, the distribution of this species is confirmed in coral reef environments associated with the coast of Quintana Roo.

Phylogenetic analysis

Partial *rbc*L sequences of 700 bp approximately were obtained from *Udotea* species. Phylogram inferred from *rbc*L sequences is shown in Figure 85. The phylogenetic analysis showed that the corticated *Udotea* species (*U. flabellum* and *U. dixonii*) are not closely related to the uncorticated species (*U. conglutinata*, *U. cyathiformis* var. *flabellifolia*, *U. looensis*, *U. luna* and *U. spinulosa*). Instead the last species were clustered with *Penicillus capitatus* and *Rhipocephalus phoenix* f. *brevifolius* confirming the polyphyletic origin of *Udotea* genus. The phylogram contained four major clades. The first clade contained the corticated species (*U. flabellum* and *U. dixonii*), meanwhile the second one contained only a corticated species (*U. spinulosa*) with blade appendages with a short peduncle, which a total of 1–8 spine-like projections arose. The third clade contained uncorticated species with a swollen and apiculate lateral appendages of

stipe siphons (*U. conglutinata*, *U. looensis* and *U. luna*). The fourth clade contained *Penicillus capitatus*, *Rhipocephalus phoenix* f. *brevifolius* and *Udotea cyathiformis* var. *flabellifolia*. The clusters received relatively high bootstrap support (>55%). This molecular information may indicate that the presence of the blade is not a diagnostic character to the *Udotea* genus.

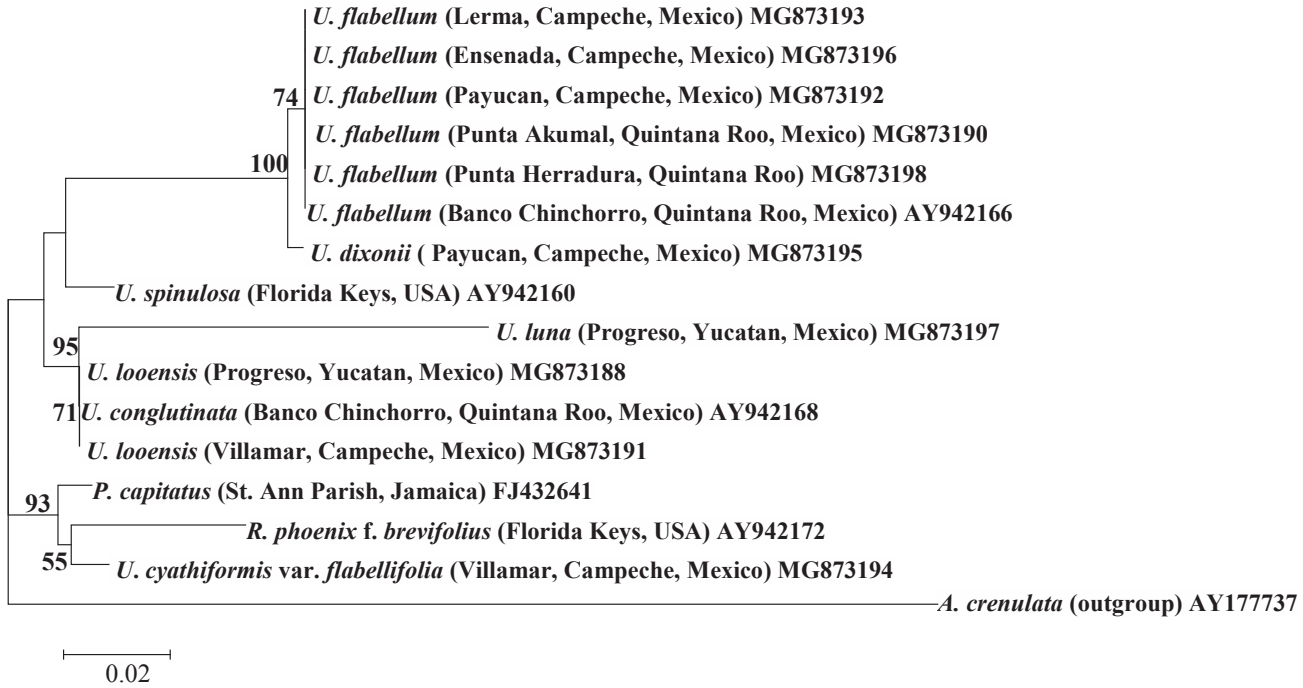


FIGURE 85. Phylogenetic tree inferred from partial *rbc*L sequences of *Udotea*, *Penicillus* and *Rhipocephalus* species.

Discussion

Diversity

The Yucatan Peninsula is a marine biogeographical area with high species richness of benthic marine algae (Fredericq *et al.* 2009, Mendoza-González *et al.* 2016), this is confirmed considering that 17 taxa of the *Udotea* genus were recorded, of the 23 described for the Western Tropical Atlantic (Guiry & Guiry 2017, Wynne 2017). Sixteen taxa of *Udotea* have been recorded in the Yucatan peninsula littoral (Huerta-Múzquiz 1958, Huerta-Múzquiz & Garza-Barrientos 1966, Taylor 1972, Garza-Barrientos 1975, Huerta-Múzquiz & Garza-Barrientos 1980, Huerta-Múzquiz *et al*. 1987, Aguilar-Rosas *et al*. 1989, Aguilar-Rosas 1990, Mendoza-González & Mateo-Cid 1992, Dreckmann *et al*. 1996, Aguilar-Rosas *et al*. 1998, Mendoza-González *et al*. 2000, Aguilar-Rosas *et al.* 2001, Ortegón-Aznar *et al.* 2001, Callejas-Jiménez *et al*. 2005, Mateo-Cid & Mendoza-González 2007, Sánchez-Molina *et al.* 2007, Collado-Vides *et al*. 2009, Rosado-Espinoza *et al*. 2012, Mateo-Cid *et al*. 2013, Ortegón-Aznar & Aguilar-Perera 2014, Acosta-Calderon *et al*. 2016, Mendoza-González *et al.* 2016). The collections made by the authors confirmed the presence of 14 taxa. *Udotea occidentalis* and *U. unistratea* were not recorded, these species have been reported at depths greater than 10 m (Littler & Littler 1990, Mendoza-González *et al*. 2000, Mendoza-González *et al.* 2013), nevertheless specimens of both species are housed in the ENCB herbarium, which allowed to corroborate their presence in the Yucatan peninsula littoral. Also, the examination of material deposited in the ENCB herbarium rejected the records of *U. verticillosa* in the Quintana Roo littoral (Huerta-Múzquiz *et al*. 1987, Mendoza-González & Mateo-Cid 1992), since various specimens assigned to this species correspond to *U. unistratea* and *U. caribaea*. *Udotea norrisii* is cited for the first time for the Yucatan peninsula littoral. The number of species known for the Campeche and Yucatan littoral increased because of the sampling effort in these regions.

Distribution

The genus *Udotea* is distributed in tropical and subtropical regions of the Pacific, Indian, and Atlantic oceans (Olsen-Stojkovich 1985, Wynne 2017, Guiry & Guiry 2017). In the Mexican coasts, this genus has been recorded only in the Quintana Roo, Yucatan, and Campeche coast (Aguilar-Rosas *et al.* 2001, Ortega *et al*. 2001, Garduño-Solórzano *et al*.

2005, Pedroche *et al*. 2005, Mendoza-González *et al*. 2016). The highest species richness of this genus was recorded in the Quintana Roo littoral, where greater diversity of stable substrates facilitates the establishment and development of *Udotea* species (Fredericq *et al*. 2009, Mendoza-González *et al*. 2016), in contrast with the Yucatan and Campeche coast, where sandy beaches with constant waves are a common habitat, so the substrate is unstable, disturbing the development of these algae (Aguilar-Rosas *et al*. 2001, Mateo-Cid *et al*. 2013). The northern region of the Yucatan peninsula littoral is considered a biogeographic barrier that divides the Gulf of Mexico from the Caribbean Sea with oceanographic, geomorphological, and biological differences among the shores that constitute it (Fernández-Equiarte *et al*. 1983, Ward *et al*. 1985, Britton & Norton 1989, De La Lanza-Espino 1991), this may explain the lower species richness of *Udotea* between the boundaries of the Yucatan and Campeche littoral.

On the other hand, the distribution of the *Udotea* genus in the Gulf of Mexico seems to be restricted to the Campeche coast, because *Udotea* specimens were not found in the bordering sampling localities of Campeche and Tabasco, besides there are no records of *Udotea* for the other states located at the Mexican Atlantic (Tabasco, Veracruz, and Tamaulipas) (Ortega *et al*. 2001, Garduño-Solórzano *et al*. 2005, González-Gándara *et al*. 2007, Robinson *et al*. 2012, Sentíes & Dreckmann 2013, García-López *et al*. 2017, Quiroz-González *et al*. 2017). The limit of the distribution of the *Udotea* genus can be potentially associated with the variations of salinity derived from the freshwater contribution by the Grijalva and Usumacinta rivers that flow into the coast of Tabasco. The Grijalva-Usumacinta system, together with the Papaloapan river, contributes 55% of the fresh water discharge in the Mexican Atlantic slope (Toledo-Ocampo 1996). Salinity variations can affect the growth, distribution, and productivity of the benthic marine algae because of osmotic stress that may inhibit these processes (Kamer & Fong 2000, Jahnke & White 2003, Xia *et al*. 2004); notwithstanding most Chlorophyta algae can tolerate salinity fluctuations; the Udoteaceae species are strictly marine (Lüning 1990, Graham & Wilcox 2000).

In this study *Udotea* species were found on subtidal rock platforms with little movement of water (*U. caribaea*, *U. fibrosa*), sandy bottoms associated to sea grass meadows (*U. abbottiorum*, *U. dixonii*) and on calcareous rocky substrate (*U. cyathiformis* f. *sublittoralis*, *U. wilsonii*), which agrees with Graham & Wilcox (2000), Aguilar-Rosas *et al*. (2001) and Collado-Vides *et al*. (2009), who mentioned that Udoteaceae species can establish on rocky, sandy, and clayey substrates with little movement of water in the subtidal zone. This ability to occupy several substrates is facilitated by its anchoring system formed by rhizoids that secrete mucilage that adheres to the background (Bedinger *et al*. 2013). *Udotea flabellum* and *U. dixonii* were widely distributed along the Yucatan peninsula coast. This ability to inhabit a greater diversity of environments is probably due to physiological aspects such as the production of secondary metabolites acting as a chemical defense mechanism against herbivores (Paul & Fenical 1986, Nakatsu *et al*. 1981), or the presence of thalli that grant resistance to mechanical disturbances such as intense waves and currents (Collado-Vides *et al*. 1998). The *U. flabellum* and *U. dixonii* talli are robust, highly calcified and with a developed rhizoidal mass, whereas thalli of *U. wilsonii* and *U. cyathiformis* are thin, scarcely calcified and restricted to reef lagoons. Littler & Littler (1990) mentioned that low calcified species are more susceptible to damage by the swell and herbivores.

Taxonomy

Traditionally, the taxonomy of macroalgae has been based on the use of morphological and anatomical characteristics of the thalli for description, delimitation, and classification of the species. However, these tasks tend to be conflicting mainly because the original descriptions of the species are not very informative, variations in the diagnostic characters, and the probable convergence and parallel evolution of some of these (Bowler & Allen 2007). In this regard, 26 morphological and anatomical characters proposed by Littler & Littler (1990) and, as complementary characters, the length and diameter of the supradichotomic constrictions and the lateral appendages of the blade and stipe siphons were used in this study to delimit the 17 taxa of *Udotea* genus in the Yucatan peninsula littoral. The consistency of the characters is fundamental for accurate taxonomic assignment (Collado-Vides 2002, de Senerport-Domis *et al.* 2003, Verbruggen *et al*. 2005). In this sense, the presence or lack of lateral appendages in the blade siphons and the shape of the lateral appendages of the blade and stipe siphons were constant qualitative characters that allowed for the recognition of the 17 *Udotea* taxa in the study area. In contrast, the blade morphology and dimensions of the diameter of the blade and stipe siphons were the characters with greater inter- and intra-specific variability. Littler & Littler (1990) mentioned that the length of the lateral appendages of *Udotea* species tends to increase as depth increases. In the present study, *U. cyathiformis, U. cyathiformis* f. *sublittoralis, U. dixonii,* and *U. norrisii* showed different external morphology respect to Littler & Littler (1990) descriptions, however the shape of the lateral appendages of the blade and stipe siphons allowed the designation of specific epithets. Also, morphological differences were found in *U. dixonii*, *U. flabellum*, *U. looensis*, *U. luna,* and *U. norrisii* specimens from different sampling locations in the Yucatan peninsula. Another character that did not coincide with the descriptions of Littler & Littler (1990) and

Collado-Vides *et al*. (2009) was the diameter of the blade and stipe. One of the important characteristics of seaweeds is their morphological plasticity, resulting in different morphologies among species according to the conditions of light, temperature, salinity, nutrients, depth, and herbivorous activity (Norton *et al*. 1981, Lobban & Harrison 1997, Collado-Vides 2002, de Senerport Domis *et al.* 2003, Verbruggen *et al*. 2005, Mateo-Cid *et al*. 2008, Verbruggen 2014). The classification of Udoteaceae species is supported by vegetative character differences in contrast to other close families such as Bryopsidaceae and Derbesiaceae, whose classification is based on vegetative and reproductive characters (Hillis-Colinvaux 1984, Vroom *et al*. 1998, Cocquyt *et al*. 2010). Molecular studies based on *rbc*L and ITS sequences revealed that the Udoteaceae family is not a monophyletic clade and the *Udotea* species included in these surveys do not belong to the same clade (Kooistra 2000, Lam & Zechmann 2006, Verbrugeen *et al.* 2009a). Hence, a phylogenetic and taxonomic reassessment of the *Udotea* genus under a molecular approach is necessary to elucidate the phylogenetic relations among the Udoteaceae species, incorporating a larger number of *Udotea* sequences and different plastidial markers. The *rbc*L and *tuf*A gene have been shown to be good molecular markers for species-level segregation in several families of the Bryopsidales due to a high rate of nucleotide substitution, which is useful for interspecific segregation (Famà *et al*. 2002, Lam & Zechman 2006, Curtis *et al*. 2008, Verbruggen *et al*. 2009b, Saunderes & Kucera 2010, Dijoux *et al*. 2012, Do Nascimento-Santos & Castro-Nunes 2015). Currently, the taxonomic study of the *Udotea* genus has received little attention and there are few descriptive works of *Udotea* species. The work of Littler & Littler (1990) is an indispensable reference for the determination of species because they presented descriptions of known and new species, and provided a taxonomic key to the genus and detailed illustrations of the morphology and anatomy of the thallus. A complementary work is that of Collado-Vides *et al.* (2009), which morphological and anatomical characteristics of *Udotea* specimens were documented, but no schemes of these characteristics were provided. Hence, this study provides new information on the recognition of species distributed in the Yucatan peninsula littoral through a greater number of assessed specimens, significant sampling effort along the study area, and the descriptions of anatomical-morphological features of specimens from the Mexican coast.

Phylogenetic analysis

Despite the wide acceptance of the used of molecular data for delimiting species and testing the traditional boundaries (Tautz *et al*. 2003, Blaxter 2004, Saunders 2008, McDevit & Saunders 2009, De Clerck *et al.* 2013, Leliaert *et al.* 2014), not many sequences of *Udotea* genus are available in public databases. This study generated 10 novel partial *rbc*L gene sequences from *Udotea*. Coenocityc green algae belonging to the traditional genera *Udotea* did not form a monophyletic group. This confirms the previous findings with other molecular data (Kooistra 2002, Lam & Zechmann 2006, Verbrugeen *et al.* 2009a, van der Loos *et al.* 2016). The genus *Udotea* is characterized by a green macroscopic coenocytic erect thalli composed by an uncalcified, basal, rhizoidal mass anchored to substrata, an upright calcified and corticated stipe and, a calcified funnel or fan shaped terminal blade (Lamouroux 1812, Howe 1904, 1909, Gepp & Gepp 1911, Taylor 1960, Littler & Littler 1990). However, all molecular evidence suggests that the presence of a blade in a terminal portion of the thalli is not the diagnostic character for the *Udotea* genus. The uncorticated species are in the same clade of the *Penicillus* and *Rhipocephalus*. The brush of *Penicillus* and imbricated blade of *Rhipocephalus* are like an uncorticated blade of *Udotea*, because no lateral appendages on the blade siphons are observed. Since the phylogeny does not support the current taxonomic division based on morphological and anatomical characters, these genera should be revised under the molecular and phylogenetic approach using sequences of 18S, ITS, *rbc*L, *tuf*A, *atp*B, 16S genes. For example, the *rbc*L and *tuf*A plastidial genes have proved to be good markers for the species delimitation of green algae Ulvophyceae (Fama *et al*. 2002, Zucarello *et al.* 2009, Verbruggen *et al.* 2009b, Saunders & Kucera 2010, Coppejans *et al.* 2011, Dijoux *et al*. 2012, van der Loos *et al.* 2017). It is imperative to generate more gene sequences of all morphological described *Udotea* species to resolve these taxonomic inconstancies.

Conclusion

Seventeen infrageneric taxa of *Udotea* were described in the study area. *Udotea norrisii* is a new record for this region. The classic generic concept based on the morphological and anatomical characters is not supported by the *rbc*L phylogeny obtained in this study. It is necessary to generate more sequences of the rest of the *Udotea* species, and related genera as *Penicillus* and *Rhipocephalus* to unravel the phylogenetic relationships and propose a new classification scheme of the species. Molecular and morphological total evidence will be useful for future taxonomic, floristic, molecular, and biogeographic studies of the *Udotea* genus in the Yucatan peninsula.

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