

## Review

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# The benthic marine algae of the tropical and subtropical Western Atlantic: changes in our understanding in the last half century

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Taylor's (1960) floristic treatment of the benthic marine algae of the tropical and subtropical western Atlantic and Wynne's (2011) "checklist: third revision" serve as benchmarks in a review of changes made in the past half-century period. There has been a great increase in the number of recognized taxa of red, brown and green algae at all taxonomic ranks: from 758 to 1,393 species, an increase of 84%; from 231 to 406 genera, an increase of 75%; and from 63 to 106 families, an increase of 68%. In regard to recognized infraspecific taxa, the increase was less dramatic, from 140 to 185, thus a 32% change in the 50-year period. This review addresses the question: What factors were responsible for this proliferation of taxa that are now recognized in this domain of the tropical and subtropical western Atlantic? The answer is that many reasons contributed to these changes. Foremost among these causes have been the advances in gene-sequencing technologies. Revised phylogenetic relationships have led to many genera being divided into more than one genus, as well as new families and orders being delineated. Numerous examples of cryptic species have been discovered by gene-sequence and DNA-bar coding studies. This trend is depicted by case studies. Examples of genera being divided are *Galaxaura*, *Liagora* and *Laurencia*. *Tricleocarpa* and *Dichotomaria* have been segregated from *Galaxaura*. *Trichogloeopsis*, *Ganonema*, *Izziella*, *Yamadaella*, and *Titanophycus* have been segregated from *Liagora*. *Chondrophycus*, *Osmundea*, *Palisada*, and *Yuzurura* have been segregated from *Laurencia*. Examples are given of other genera present in this region of the western Atlantic that have been split up. Many genera have increased in terms of the number of species now assigned to them. Taylor's (1960) treatment recognized only two species in *Hypoglossum*, whereas Wynne's (2011) checklist contained a total of 9 species of *Hypoglossum*. Taylor's account included only two species of *Botryocladia*, but this number had grown to 15 in Wynne's checklist. Examples of new genera and species occurring in the region of the western Atlantic are given, and examples of taxa being newly reported for this domain are provided. An increase in the number of phycologists in Latin and South America, exploration of previously unexplored regions, and the increasing use of SCUBA for collecting and at greater depths have all contributed to the increase in the number of algal taxa that are now recognized as occurring in the tropical and subtropical western Atlantic.

**Key Words:** historical treatment; long-term changes; marine algae; tropical and subtropical western Atlantic

The volume "*Marine algae of the eastern tropical and subtropical coasts of the Americas*" produced by W. R. Taylor in 1960 was a comprehensive treatment of the benthic seaweeds of this region and remains a useful compendium for the breadth of its coverage, its detailed descriptions, and excellent artwork. But in the 50 years since that floristic treatment, numerous regional treatments have appeared, many new taxa described, and many new records have been published. Wynne has produced several checklists over the years (1986, 1998, 2005) in efforts to gather the pertinent literature from

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this broad region from Cape Hatteras, North Carolina, in the north to southern Brazil in the south. The recently published third revision of this checklist (Wynne 2011) gives us the opportunity to see the dramatic changes in the schemes of classification and in the treatment of genera of red, brown, and green algae from the new information provided by the flood of phylogenetic data. This paper reviews important changes with specific and more general examples.

Table 1 provides a comparison of the numbers of taxa (families, genera, species, and infraspecific taxa) of red, brown, and green algae in Taylor (1960) and in Wynne (2011), giving the total numbers in each category and also showing the percent increases between these two chosen benchmarks.

**Table 1.** A comparison of the numbers of taxa (families, genera, species, and infraspecific taxa) of red, brown, and green algae in Taylor (1960) and in Wynne (2011)

	Family		Genus		Species		Infraspecific taxa	
	Taylor (1960)	Wynne (2011)	Taylor (1960)	Wynne (2011)	Taylor (1960)	Wynne (2011)	Taylor (1960)	Wynne (2011)
Rhodophyta	31	58	133	255	454	905	44	55
Heterokontophyta	15	18	45	76	101	175	15	33
Chlorophyta	17	30	53	75	203	313	81	97
Total	63	106	231	406	758	1,393	140	185
Increase (%)		68		75		84		32

This review addresses the question of what factors were responsible for the significant increases in the percentages of taxa recognized in the past half century for the marine algal flora of the western Atlantic. The fact is that many reasons have played a role in the expansion of our knowledge. The technology of gene-sequencing and the employment of those data to understand phylogenetic relationships have been foremost among the causes for the increase in the number of taxa at all levels. New information has resulted in broad realignments with respect to how the orders and classes of these groups are interrelated. Many red algal orders have been delineated since the time of Taylor’s (1960) floristic treatment, especially among the subclass Bangiophycidae. Only seven orders of red algae were recognized in Taylor’s (1960) treatment, and those orders were assigned to a single class (Rhodophyceae) with two sub-classes (Bangioideae and Florideae). In Wynne’s (2011) treatment the red algae are assigned to six classes, and the Florideophyceae, the largest class, contains 21 orders at the present time. The most species-rich order, the Ceramiales, is no longer considered necessarily to be the most derived (Yoon et al. 2006, Le Gall and Saunders 2007, Maggs et al. 2007), and the former broadly defined family Ceramiaceae has been split up into four families in this checklist (Choi et al. 2008).

On the other hand, molecular-based evidence has resulted in the amalgamation of many families of brown algae into a broadly circumscribed Chordariaceae (Peters and Ramirez 2001) and several orders of brown algae (Chordariales, Dictyosiphonales, and Scytosiphonales) into a broadly circumscribed order Ectocarpales (Draisma et al. 2003, Cho et al. 2004). Likewise, radically different views of how brown algal orders are interrelated have been proposed, again due to recent molecular studies, and the Laminariales and Fucales are no longer placed in the more derived positions in the evolutionary scheme (Draisma et al. 2001, Rousseau et al. 2001, Cho et al. 2004, Kawai et al. 2007, Reviers et al. 2007, Phillips et al. 2008). Higher-level rearrangements in the green algae reflect the results of recent molecular-based phylogenetic analyses (Lam and Zechman 2006, Pröschold and Leliaert 2007, Curtis et al. 2008, Zechman et al. 2010).

More exacting methods and closer scrutiny, often making use of molecular-sequencing technologies, have led to the recognition that some genera are best divided into more than one genus. These revised arrangements better reflect more accurate phylogenetic relationships. This trend over the past half century is demonstrated with the examples of the genera *Galaxaura*, *Liagora*, and *Laurencia*.

**Changes in our concept of *Galaxaura* over the past 50 years:**

Taylor (1960)	Wynne (1986)	Wynne (1998)	Wynne (2005)	Wynne (2011)
<i>Galaxaura</i>	<i>Galaxaura</i>	<i>Galaxaura</i>	<i>Galaxaura</i>	<i>Galaxaura</i>
14 spp.	6 spp.	5 spp.	2 spp.	2 spp.
		<i>Tricleocarpa</i>	<i>Tricleocarpa</i>	<i>Tricleocarpa</i>
		2 spp.	2 spp.	2 spp.
			<i>Dichotomaria</i>	<i>Dichotomaria</i>
			2 spp.	2 spp.

Taylor (1960) referred to the fact then known in a preliminary way that some of the taxa of *Galaxaura* were “species pairs” representing dimorphic gametophytic and sporophytic phases of the same species. Howe (1917) had earlier recognized that in the West Indian *G. obtusata* the gametophytes and tetrasporophytes are markedly different in the structure of their cortex, such that they would fall into two different species on the basis of Kjellman's (1900) monograph of the genus. The reduction of the relatively large number (14) species of *Galaxaura* recognized by Taylor (1960) to only 6 species in Wynne (1986) was a reflection of the monographic treatment by Papenfuss et al. (1982). Dimorphic gametophytic and sporophytic stages in *Galaxaura rugosa* (J. Ellis et Sol.) J. V. Lamour. (Figs 1 & 2) were recognized by Littler and Littler (2000). The next major change in the circumscription of *Galaxaura* was made by Huisman and Borowitzka (1990), who separated off some species into the new segregate genus *Tricleocarpa* based on morphological, reproductive, and life history differences. Species of *Tricleocarpa*, including *T. cylindrica* (J. Ellis et Sol.) Huisman & Borow. (Fig. 3) and *T. fragilis* (L.) Huisman & R. A. Townsend (Fig. 4), were distinguished by a life history showing an alternation of heteromorphic phases, involving a microscopic filamentous tetrasporophyte alternating with a dominant gametophytic phase, in contrast to the alternation of isomorphic phases expressed in *Galaxaura sensu stricto*. Later, Huisman et al. (2004b) offered evidence for the reinstatement of the genus *Dichotomaria* Lamarck, lectotypified with *D. marginata* (J. Ellis et Sol.) Lam. (Fig. 5), and for the transfer of some species of *Galaxaura* into that reinstated genus. Recognition of *Dichotomaria* avoided a situation in which *Galaxaura* would be para / polyphyletic based on the gene-sequence results. A second species now recognized as assigned to *Dichotomaria* is *D. obtusata* (J. Ellis et Sol.) Lam. (Fig. 6).

#### Changes in our concept of *Liagora* over the past 50 years:

Taylor (1960)	Wynne (1986)	Wynne (1998)	Wynne (2005)	Wynne (2011)
<i>Liagora</i>	<i>Liagora</i>	<i>Liagora</i>	<i>Liagora</i>	<i>Liagora</i>
9 spp.	11 spp.	9 spp.	5 spp.	4 spp.
	<i>Trichogloeopsis</i>	<i>Trichogloeopsis</i>	<i>Trichogloeopsis</i>	<i>Trichogloeopsis</i>
	1 sp.	1 sp.	1 sp.	1 sp.
		<i>Ganonema</i>	<i>Ganonema</i>	<i>Ganonema</i>
		1 sp.	5 sp.	6 sp.
			<i>Izziella</i>	<i>Izziella</i>
			1 sp.	1 sp.
			<i>Yamadaella</i>	<i>Yamadaella</i>
			1 sp.	1 sp.
				<i>Ttanophycus</i>
				1 sp.

A total of nine species of *Liagora* were recognized by Taylor (1960), including *L. ceranoides* J. V. Lamour. (Fig. 7). The first move to break *Liagora* into a number of the genera now recognized was made by Abbott and Doty (1960), who recognized the segregate genus *Trichogloeopsis* distinguished by its possession of sterile rhizoids produced by the gonimoblast and by the fact that the carpogonial branch was a modified vegetative filament, in contrast to the accessory (specialized) carpogonial branch in *Liagora sensu stricto*. *Trichogloeopsis* was typified by *T. hawaiiiana* and also included *T. pedicellata* (M. Howe) I. A. Abbott et Doty (Fig. 8). Although the segregate genus *Ganonema* was established by Fan and Wang (1974), at first Abbott (1984) offered arguments to merge it back within *Liagora*. But Huisman and Kraft (1994) subsequently presented persuasive evidence for the recognition of *Ganonema* with an emended definition. Although the generitype *Ganonema farinosum* (J. V. Lamour.) K. C. Fan et Yung C. Wang (Fig. 9) was the only species recognized as occurring in the western Atlantic by Wynne (1998), four other species have been assigned to the genus by Wynne's (2005) second revision: *G. dendroideum* (P. Crouan et H. Crouan) D. L. Ballant. et Aponte (Ballantine and Aponte 2002b) (Fig. 10), *G. megagynum* (Børgesen) Huisman and *G. pinnatum* (Harv.) Huisman (both transfers made by Huisman 2002), and *G. norrisiae* (I. A. Abbott) Huisman, I. A. Abbott et A. R. Sherwood (Huisman et al. 2004a). A new species of *Ganonema*, *G. vermiculare*, was described from Puerto Rico by Ballantine and Abbott (2006).

The genus *Izziella* was established by Doty (1978). Abbott (1990), however, offered reasons to merge the genus within *Liagora* and treated the type species of *Izziella*, *I. abbotiae* Doty, as conspecific with *L. orientalis* J. Agardh. She reported the presence of *L. orientalis* from Puerto Rico and Colombia. Later, Huisman and Schils (2002) recognized notable dif-

ferences in the type species of *Izziella* from *L. viscida* (Forsskål) C. Agardh, the generitype of *Liagora*, and thus reinstated *Izziella*. *Yamadaella* was segregated from *Liagora* by Abbott (1970), with the single species, *Y. caenomyce* (Decne.) I. A. Abbott (Fig. 11), and the genus remains monotypic. Although the genus was known from many records throughout the tropical Indo-Pacific, its first report to occur in the western Atlantic was made by Wynne and Huisman (1998) with a collection from the Dominican Republic. *Liagora valida* Harv., with a type locality of Sand Key, Florida, USA, was separated into its own genus, *Titanophycus*, by Huisman et al. (2006) on the basis of gene-sequence evidence. At this time the genus remains monotypic, with *T. validus* (Harv.) Huisman, G. W. Saunders et A. R. Sherwood (Fig. 12).

#### Changes in our concept of the genus *Laurencia* over the past 50 years:

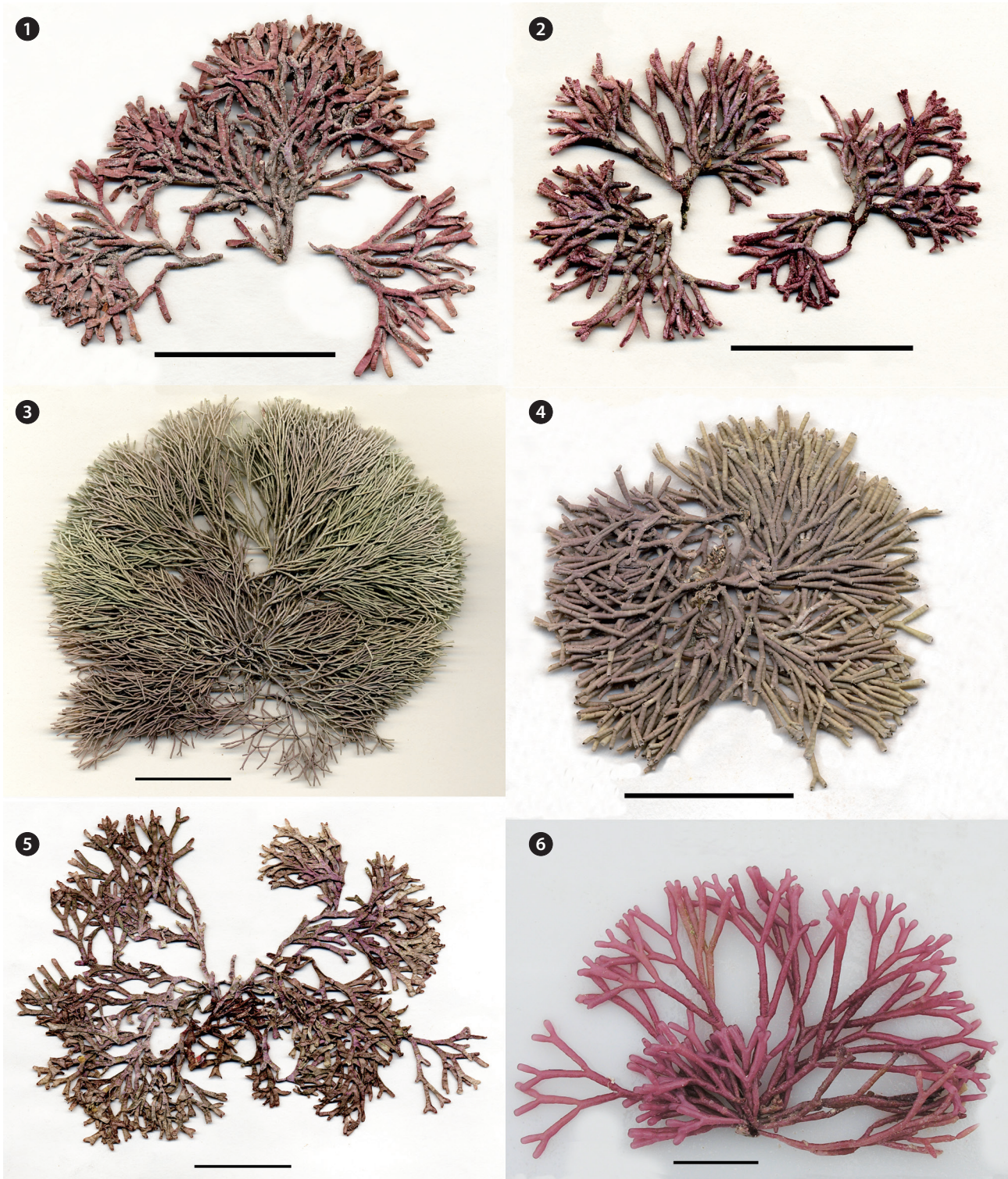
Taylor (1960)	Wynne (1986)	Wynne (1998)	Wynne (2005)	Wynne (2011)
<i>Laurencia</i>	<i>Laurencia</i>	<i>Laurencia</i>	<i>Laurencia</i>	<i>Laurencia</i>
11 spp.	22 spp.	32 spp.	23 spp.	24 spp.
			<i>Chondrophyucus</i>	<i>Chondrophyucus</i>
			9 sp.	1 sp.
			<i>Osmundea</i>	<i>Osmundea</i>
			3 sp.	4 sp.
				<i>Palisada</i>
				5 spp.
				<i>Yuzurura</i>
				1 sp.

The subdivision of *Laurencia sensu lato* into several segregate genera began with the proposal of Nam et al. (1994) to reinstate *Osmundea* Stackhouse (1809), with *O. pinnatifida* (Hudson) Stackhouse as generitype. This was followed by the proposal made by Garbary and Harper (1998) for the elevation of subgenus *Chondrophyucus* of Tokida and Saito (Saito 1967) to generic status. Wynne's (2005) treatment recognized 3 species of *Osmundea* and 9 species of *Chondrophyucus*. Later, Abe et al. (2006) and others had shown with molecular phylogenetic evidence that the species recognized within *Chondrophyucus* formed two separate clades. Nam (2006) offered both morphological and molecular evidence to recognize the segregate genus *Palisada* at the generic level. Nam's initial proposal to recognize *Palisada* as a segregate genus was invalid as were his proposed transfers of many species to that genus. Subsequently, Nam (2007) satisfied the requirements of the International Code of Botanical Nomenclature. Martin-Lescanne offered evidence to elevate Nam's (1999) subgenus *Yuzurua*, with the single species *Y. poiteaui* (J. V. Lamour.) Martin-Lescanne, to the generic level, segregated from *Palisada* on both molecular and morphological evidence (Martin-Lescanne et al. 2010).

The following species have been attributed to *Laurencia sensu stricto* in the flora of the western Atlantic post-1960: *L. aldingensis* Saito et Womersley (Carvalho et al. 2003), *L. caduciramulosa* Masuda et Kawaguchi (Cassano et al. 2006, Senties et al. 2010), *L. catarinensis* Cord. -Mar. et Fujii (1985), *L. coelenterata* D. L. Ballantine et Aponte (1995), *L. decumbens* Kütz. (Oliveira and Ugadim 1974, Rodríguez de Rios and Lobo 1984, both as *L. pygmaea*), *L. epiphylla* Boisset et Lino (Areces et al. 2003), *L. foldatsii* (Rodríguez de Rios 1981), *L. hancockii* E. Y. Dawson (Huerta and Garza 1980), *L. marilzae* Gil-Rodríguez et al. (Rocha-Jorge et al. 2010, Senties et al. 2011), *L. minuscula* (Schnetter 1975), *L. oliveirana* (Yoneshigue 1985), *L. translucida* Fujii et Cord. -Mar. (1996), and *L. venusta* Yamada (Senties et al. 2001, Fujii et al. 2005). The name *L. scoparia* J. Agardh, which had been listed in Taylor (1960), has been replaced in Wynne (2011) by *L. dendroidea* J. Agardh, the older taxonomic synonym. Fujii et al. (2006) used *rbcL* sequence data to show that Brazilian specimens going under the names *L. scoparia*, *L. arbuscula*, and *L. filiformis* do not show significant genetic variation. They concluded that these taxa likely represent a single morphologically variable species in Brazil. Cassano (2009) eliminated the Australian-based *L. filiformis* (C. Agardh) Mont. from the Brazilian flora. The presence of *L. brongniartii* in the flora was confirmed by Saito and Womersley (1974). Silva (1972) proposed the name *L. caraibica* to replace the illegitimate name *L. nana* M. Howe.

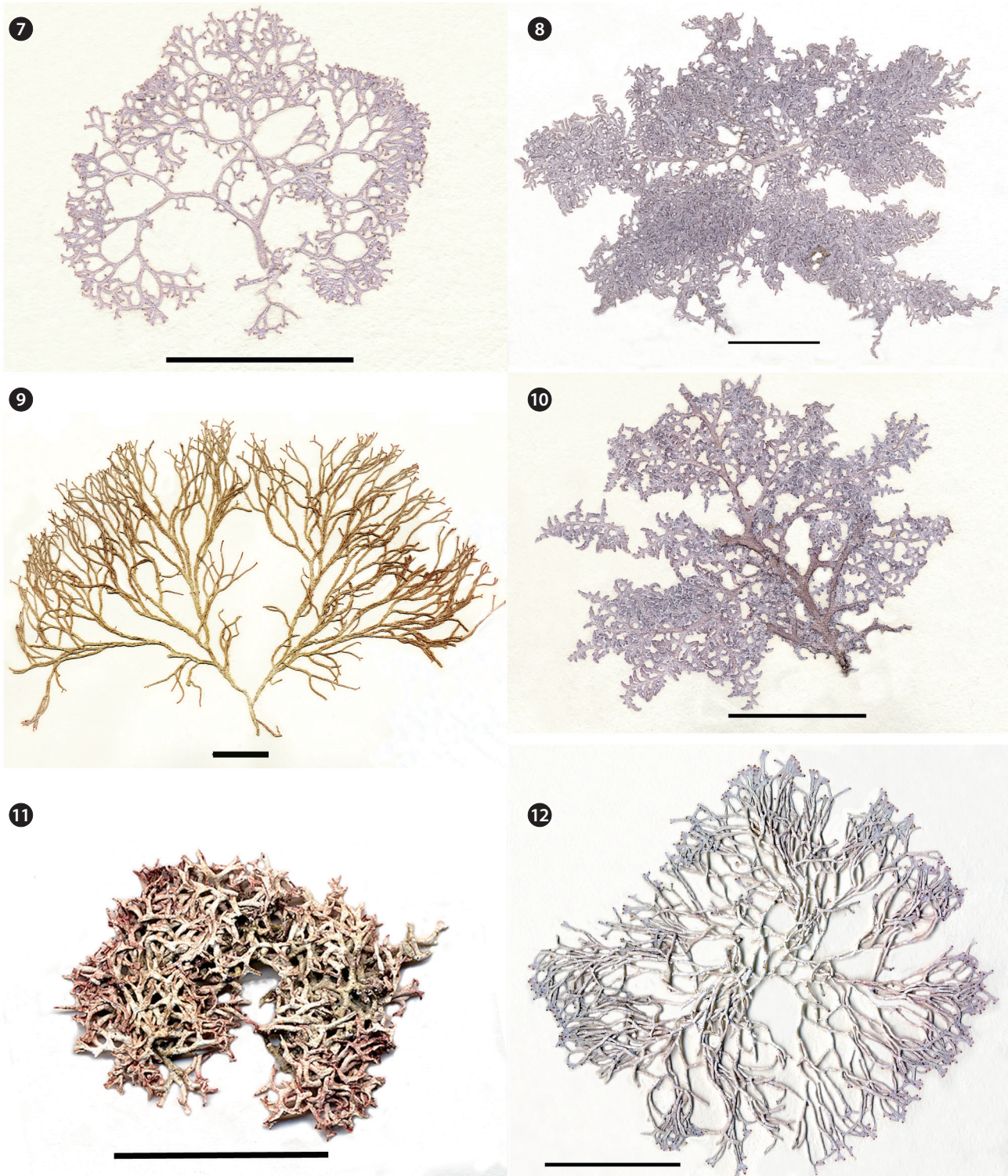
*Chondrophyucus furcatus* (Cord. -Mar. et M. T. Fujii) M. T. Fujii et Senties is the only species currently assigned to that genus for the western Atlantic (Fujii and Senties 2005). Four species of *Osmundea* are at present recognized as occurring in the western Atlantic: *O. lata* (M. Howe et W. R. Taylor) Yonesh., M. T. Fujii et Gurgel (Yoneshigue-Valentin et al. 2003), *O. oederi* (Gunnerus) G. Furnari in Serio et al. (2008), *O. pinnatifida* (Huds.) Stackh., and *O. sinicola* (Setch. et N. L. Gardner) K. W. Nam (in Nam et al. 1994) (Dawson 1962). Serio et al. (2008) proposed treating *Laurencia bolivarii* Rodríguez de Rios (1981) as conspecific with *O. oederi*.





**Figs 1-6.** **Fig. 1.** *Galaxaura rugosa*. Gametophytic plant. [Guadeloupe, M. Wynne 8245]. **Fig. 2.** *G. rugosa*. Tetrasporophytic plant. [Guadeloupe, M. Wynne 8308]. **Fig. 3.** *Tricleocarpa cylindrica*. [Dominican Republic, M. Wynne 9900]. **Fig. 4.** *T. fragilis*. [St. Kitts, M. Wynne 10501]. **Fig. 5.** *Dichotomaria marginata*. [Guadeloupe, M. Wynne 8138]. **Fig. 6.** *D. obtusata*. [Bermuda, C. Schneider & C. Lane 09-34-19]. Scale bars represent: Figs 1-6, 3 cm.





**Figs 7-12.** **Fig. 7.** *Liagora ceranoides*. [Bahamas, M. Wynne 11084]. **Fig. 8.** *Trichogloeopsis pedicellata*. [Puerto Rico, M. Wynne 11063]. **Fig. 9.** *Ganonema farinosum*. [Puerto Rico, M. Wynne 10982]. **Fig. 10.** *G. dendroideum*. [Bahamas, M. Wynne 11700]. **Fig. 11.** *Yamadaella caenomyce*. [Dominican Republic, M. Wynne 9846]. **Fig. 12.** *Titanophycus validus*. [Puerto Rico, M. Wynne 11059]. Scale bars represent: Figs 7-12, 3 cm.

Five species are currently assigned to *Palisada* for the western Atlantic: *P. corallopsis* (Mont.) Senties, M. T. Fujii et Díaz (Senties and Díaz-Larrea 2008), *P. flaglifer* (J. Agardh) K. W. Nam (Cordeiro-Marino 1978, Nam 2007), *P. intermedia* (Yamada) K. W. Nam (Rodríguez de Rios and Saito 1982, Nam 2007), *P. iridescens* (M. J. Wynne et D. L. Ballant.) K. W. Nam (Wynne and Ballantine 1991, Nam 2007) (Figs 41-43), and *O. perforata* (Bory) K. W. Nam (Nam 2007). Evidence has been presented by Cassano et al. (2009) to treat *Palisada* [*Laurencia*] *papillosa* as a taxonomic synonym of *P. perforata*. *Yuzurua* is a monotypic genus (Martin-Lescanne et al. 2010), and *Y. poiteau* contains the var. *gemmifera* (Harv.) M. J. Wynne (2011) based on the evidence presented by Díaz-Larrea et al. (2007) to treat *Chondrophycus gemmiferus* as a variety within *C. poiteau*.

**Other examples of the recognition of segregated genera and reference(s):**

<i>Neosiphonia</i> out of <i>Polysiphonia</i>	(Kim and Lee 1999, Guimarães et al. 2004)
<i>Parviphycus</i> out of <i>Gelidiella</i>	(Santelices 2004)
<i>Preroccladiella</i> out of <i>Pterocladia</i>	(Santelices and Hommersand 1997)
<i>Asteromenia</i> out of <i>Fauchea</i>	(Huisman and Millar 1996, Saunders et al. 2006)
<i>Gayliella</i> out of <i>Ceramium</i>	(Cho et al. 2008)
<i>Tiffaniella</i> out of <i>Spermothamnion</i>	(Doty and Meñez 1960)
<i>Frikkiella</i> out of <i>Branchioglossum</i>	(Wynne and Schneider 1996)
<i>Hydropuntia</i> out of <i>Gracilaria</i>	(Wynne 1989, Gurgel and Fredericq 2004)
<i>Canistrocarpus</i> out of <i>Dictyota</i>	(De Clerck et al. 2006)
<i>Feldmannia</i> out of <i>Ectocarpus</i>	(Hamel 1939, Knoepffler-Péguy 1970)
<i>Asteronema</i> out of <i>Ectocarpus</i>	(Delépine and Asensi 1975)
<i>Neoralgsia</i> out of <i>Ralfsia</i>	(Lim et al. 2007)
<i>Asterocladon</i> out of <i>Ectocarpus</i>	(Müller et al. 1999)
<i>Gayralia</i> out of <i>Monostroma</i>	(Vinogradova 1969)
<i>Blidingia</i> out of <i>Enteromorpha/Ulva</i>	(Kylin 1947)
<i>Pedobesia</i> out of <i>Derbesia</i>	(MacRaid and Womersley 1974, Wynne and Leliaert 2001)
<i>Phyllodictyon</i> out of <i>Struvea</i>	(Kraft and Wynne 1996)
<i>Caulerpella</i> out of <i>Caulerpa</i>	(Prud'homme van Reine and Lokhorst 1992, Famà et al. 2002)
<i>Parvocaulis</i> out of <i>Acetabularia</i>	(Berger et al. 2003)

The above examples of the splitting up of genera and also the recognition of cryptic species accounts for the increase in number of taxa. But the merger of genera is another reality, with such examples:

<i>Pseudogloiophloea</i> into <i>Scinaia</i>	(Huisman 1985)
<i>Gelidiopsis</i> into <i>Ceratodictyon</i>	(Norris 1987, Le Gall et al. 2008)
<i>Dilophus</i> into <i>Dictyota</i>	(Hörnig et al. 1992)
<i>Enteromorpha</i> into <i>Ulva</i>	(Hayden et al. 2003)
<i>Cystodictyon</i> into <i>Anadyomene</i>	(Littler and Littler 1991)
<i>Acicularia</i> into <i>Acetabularia</i>	(Bailey et al. 1976)

There are multiple reasons for the great increase in the number of species in known genera. One obvious explanation has been the exploration in areas that had not been previously explored and also the greater utilization of SCUBA and at greater depths. The number of practicing phycologists has greatly increased, especially in Cuba, Mexico, Colombia, Venezuela, and Brazil. The routine employment of gene-sequencing methods and DNA bar-coding has frequently resulted in the appreciation of “cryptic species,” whereby what might have been thought to be a single often widespread species proved to be composed of multiple species, some of which might be undescribed while in other cases names that had been thought to be taxonomic synonyms might have to be reinstated. This has happened with such species as *Centroceras clavulatum* (Won et al. 2009) and *Gracilaria tikvahiae* (Gurgel et al. 2004c) and in such genera as *Codium* (Verbruggen et al. 2007a). Kooistra and Verbruggen (2005) recognized the existence of “species pairs” in certain species of *Halimeda* such that Atlantic and Pacific sibling species could be recognized.



**Examples of the increase in the number of species recognition in selected genera:**Species of *Hypoglossum* recognized in the western Atlantic for the past 50 years:

Taylor (1960)	Wynne (1986)	Wynne (1998)	Wynne (2005)	Wynne (2011)
<i>H. involvens</i>	<i>H. involvens</i>	<i>H. involvens</i>	<i>H. involvens</i>	<i>H. involvens</i>
<i>H. tenuifolium</i>	<i>H. tenuifolium</i>	<i>H. tenuifolium</i>	<i>H. tenuifolium</i>	<i>H. tenuifolium</i>
	<i>H. anomalum</i>	<i>H. anomalum</i>	<i>H. anomalum</i>	<i>H. anomalum</i>
	<i>H. hypoglossoides</i>	<i>H. hypoglossoides</i>	<i>H. hypoglossoides</i>	<i>H. hypoglossoides</i>
		<i>H. caloglossoides</i>	<i>H. caloglossoides</i>	<i>H. caloglossoides</i>
		<i>H. rhizophorum</i>	<i>H. rhizophorum</i>	<i>H. rhizophorum</i>
		<i>H. simulans</i>	<i>H. simulans</i>	<i>H. simulans</i>
		<i>H. subsimplex</i>	<i>H. subsimplex</i>	<i>H. subsimplex</i>
			<i>H. barbatum</i>	<i>H. barbatum</i>

The tally of species of *Hypoglossum* recognized as present in the western Atlantic has grown considerably since the two species included in Taylor's (1960) treatment, *H. involvens* and *H. tenuifolium* (Figs 13 & 15), both described from Key West, Florida, USA, by Harvey (1853). The European-based type of the genus, *H. hypoglossoides* (Stackhouse) Collins et Herv. (Wynne 1984) has been widely reported in the western Atlantic, including Bermuda (Schneider 2000) (Figs 18-20), Cuba (Martínez-Daranas et al. 2002), Colombia (Díaz-Pulido and Díaz-Ruiz 2003), and Brazil (Horta et al. 2003). *Hypoglossum anomalum* was described by Wynne and Ballantine (1986) (Figs 14, 16 & 17), with a type locality of La Parguera, Puerto Rico. It was later recorded from the Bahamas (Ballantine and Aponte 2005), Brazil (Horta and Oliveira 2001), and the Dry Tortugas of Florida (Dawes and Mathieson 2008) as well as Australia and the Indo-Pacific. Although *Hypoglossum caloglossoides* was described by Wynne and Kraft (1985) from Lord Howe Island in the South Pacific, it was later reported by Bucher et al. (1990) to occur at Molasses Reef, the Florida Keys, USA, and has also been reported from Bermuda (Schneider 2004) (Figs 27 & 28), the Bahamas (Ballantine and Aponte 2005), and Puerto Rico (Ballantine et al. 2009). *Hypoglossum rhizophorum* (Fig. 26) was described from La Parguera, Puerto Rico, by Ballantine and Wynne (1988) with later records from Florida (Ballantine 1996), Bermuda (Schneider 2000), and the Bahamas (Ballantine and Aponte 2005). *Hypoglossum simulans* (Figs 21 & 22) was described by Wynne et al. (1989) from Guadeloupe, French West Indies, and later from the Bahamas (Ballantine and Aponte 2005). There are many records also from the tropical Indo-Pacific. *Hypoglossum subsimplex* (Figs 24 & 25) was described from Content Key in the Florida Keys, USA, by Wynne (1994) and was later reported to occur in the Serrana Bank, southwestern Caribbean off Nicaragua (Díaz-Pulido and Bula-Meyer 1997), Bermuda (Schneider 2000) and Puerto Rico (Ballantine et al. 2002). Finally, Schneider (2000) reported the presence of *Hypoglossum barbatum* Okamura in Bermuda (Fig. 23). This record represented the first report of this species, originally described from Hyuga, Miyazaki Pref., Japan (Okamura 1901), from the Atlantic Ocean. At the same time Schneider (2000) referred to its possible presence in Florida, although the determination was uncertain.

**Species of *Botryocladia* from the tropical / subtropical western Atlantic recognized in the past 50 years:**

Taylor (1960)	Wynne (1986)	Wynne (1998)	Wynne (2005)	Wynne (2011)
<i>B. occidentalis</i>	<i>B. occidentalis</i>	<i>B. occidentalis</i>	<i>B. occidentalis</i>	<i>B. occidentalis</i>
<i>B. pyriformis</i>	<i>B. pyriformis</i>	<i>B. pyriformis</i>	<i>B. pyriformis</i>	<i>B. pyriformis</i>
	<i>B. monoica</i>	<i>B. monoica</i>	<i>B. monoica</i>	<i>B. monoica</i>
	<i>B. papenfussiana</i>	<i>B. papenfussiana</i>	<i>B. papenfussiana</i>	<i>B. papenfussiana</i>
	<i>B. shanksii</i>	<i>B. shanksii</i>	<i>B. shanksii</i>	<i>B. shanksii</i>
	<i>B. spinulifera</i>	<i>B. spinulifera</i>	<i>B. spinulifera</i>	<i>B. spinulifera</i>
	<i>B. wynnei</i>	<i>B. wynnei</i>	<i>B. wynnei</i>	<i>B. wynnei</i>
		<i>B. ganesanii</i>	<i>B. ganesanii</i>	<i>B. ganesanii</i>
			<i>B. bahamense</i>	<i>B. bahamense</i>
			<i>B. ballantinei</i>	<i>B. ballantinei</i>
			<i>B. caraibica</i>	<i>B. caraibica</i>
				<i>B. bermudana</i>
				<i>B. exquisita</i>
				<i>B. flockii</i>
				<i>B. iridescens</i>

Only two species of *Botryocladia*, *B. occidentalis* (Børgesen) Kylin and *B. pyriformis* (Børgesen) Kylin, were recognized as present in the western Atlantic by Taylor (1960). By the time of Wynne's (1986) first checklist, five species had been added to the flora: *B. monoica* Schnetter (1978) with a type locality near Punta de Betin, Santa Marta, on the Caribbean coast of Colombia; *B. papenfussiana* Ganesan et Lemus (1972) with a type locality of Peñoncito, Cumaná, Venezuela; *B. shanksii* E. Y. Dawson (1962) with a type locality of Puerto Limon, Atlantic coast of Costa Rica, *B. spinulifera* W. R. Taylor et I. A. Abbott (1973) (Fig. 29) with a type locality of Grass Point, St. Croix, U.S. Virgin Islands, and *B. wynnei* D. L. Ballant. (Ballantine 1985) (Fig. 30) with a type locality 5 km offshore La Parguera, Puerto Rico. In the first revision (Wynne 1998) one more species had been added, *B. ganesanii* Aponte Díaz (1988) with a type locality of Pampatar, Isla de Margarita, Venezuela. Three species were added to the second revision (Wynne 2005): *B. bahamensis* D. L. Ballant. et Aponte (2002a) with a type locality of Lee Stocking Island, the Bahamas; *B. ballantinei* Gavio et Fredericq (2005) with a type locality at 60-70 m depth offshore Louisiana, USA; and *B. caraibica* Gavio et Fredericq (2003) with a type locality of Bocas del Toro, Isla Colón, Caribbean Panama. Four more species had been described by the time of Wynne's (2011) third revision. Schneider and Lane (2008), using both morphological and molecular analyses, added three newly described species of *Botryocladia* all from Bermuda: *B. bermudana* (Fig. 31) with a type locality of Hunt Island, Port Royal Bay; *B. equisita* (Figs 33 & 34) with a type locality of Bermuda Aquarium reef tank, Harrington Sound, and *B. flookii* (Fig. 32) with a type locality of Walsingham Pond, Hamilton Parish. Schneider and Lane (2008) referred to several of these new species, *B. bahamense*, *B. ballantinei*, *B. bermudana* and *B. caraibica* as member of the Greater Caribbean "*B. pyriformis*-complex." Modern molecular methods of gene-sequencing are teasing apart these cryptic taxa into distinguishable species. Ballantine and Ruiz (2008) described *B. iridescens* (Figs 35-37) with a type locality of La Parguera, Puerto Rico.

### Examples of newly described taxa post-1960:

Numerous new genera, based upon types occurring in the tropical and subtropical Western Atlantic, have been described in the past five decades. The following new genera are listed according to their phylum:

Rhodophyta: *Augophyllum* Lin et al. (2004), *Calliclavula* Schneider in Searles and Schneider (1989), *Calonitophyllum* Aregood (1975), *Crassitegula* Schneider et al. (2006), *Cresia* Lozada-Troche et al. (2010), *Crouanophycus* Athanasiadis (1998), *Diplothamnion* Joly et Yamaguishi in Joly et al. (1966), *Erythrolobus* Scott et al. (2006), *Frikkiella* Wynne et Schneider (1996), *Heterodasya* Joly et Oliveira (1966), *Liagorothamnion* Huisman et al. (2001), *Nwynnea* Searles in Searles and Schneider (1989), *Pseudobangia* Müller et Sheath in Müller et al. (2005), *Renouxia* Fredericq et Norris (1995), *Rhododictyon* Taylor (1961), *Rhodogorgon* Norris et Bucher (1989), *Waldoia* Taylor (1962b)

Heterokontophyta: *Cladophyllum* Bula-Meyer (1980), *Elachistiella* Cassano et al. (2004), *Hummia* Fiore (1975), *Jolyna* Guimarães in Guimarães et al. (1986), *Onslowia* Searles in Searles and Leister (1980), *Verosphacela* Henry (1987)

Chlorophyta: *Pseudoderbesia* Calderón et Schnetter (1991), *Smithsoniella* Sears et Brawley (1982), *Verdigellas* Ballantine et Norris (1994)

Several genera of red algal parasites have been described, such as *Dawsoniocolax* Joly et Yamaguishi-Tomita (1967, 1970), *Grateloupiocolax* Schnetter et al. (1983), *Champiocolax* Bula-Meyer (1985), *Centrocerocolax* Joly (1966), *Spyridiocolax* Joly et Oliveira (1966), *Meridiocolax* Morrill (1976). The parasitic genus *Gelidiocolax*, which was not included in Taylor (1960), was added to the flora by the descriptions of *G. desikacharyi* (Ganesan 1970) and *G. pustulata* (Yoneshigue and Oliveira 1984). The report of *Pterocladiphila* in the Caribbean by Stegenga and Vroman (1986) added that parasitic red alga to the flora.

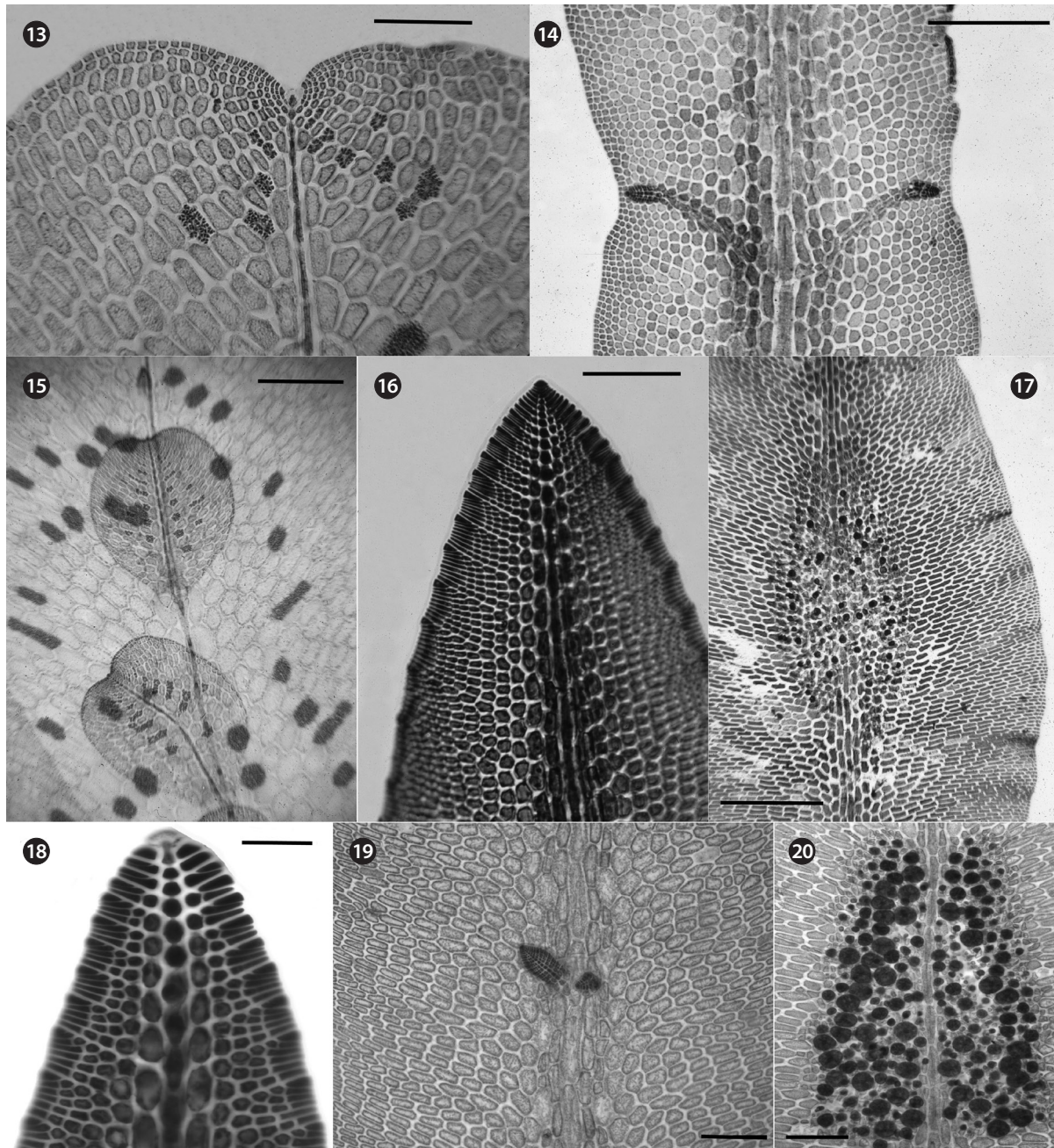
On the other hand, some genera newly described in recent years have been relegated to taxonomic synonymy. Examples are the merger of *Johnson-sea-linkia* (Eiseman and Earle 1983) into *Rhipiliopsis* proposed by Norris and Blair (in Norris and Olsen 1991) and the merger of *Siphonoclatrus* Earle et Young (1972) into *Rhipiliopsis* proposed by Farghaly and Denizot (1979).

*Meristiella* was initially segregated from *Eucheuma* (Cheney in Gabrielson and Cheney 1987), but later its merger into *Meristotheca* was proposed by Faye et al. (2004).

*Mesothamnion* (Børgesen 1917), a genus that was recognized by Taylor (1960), was initially merged within *Pleonosporium* by Norris (1985) but was later merged within *Spongoconium* (Sonder 1855) from the evidence presented by Womersley and Wollaston (1998).

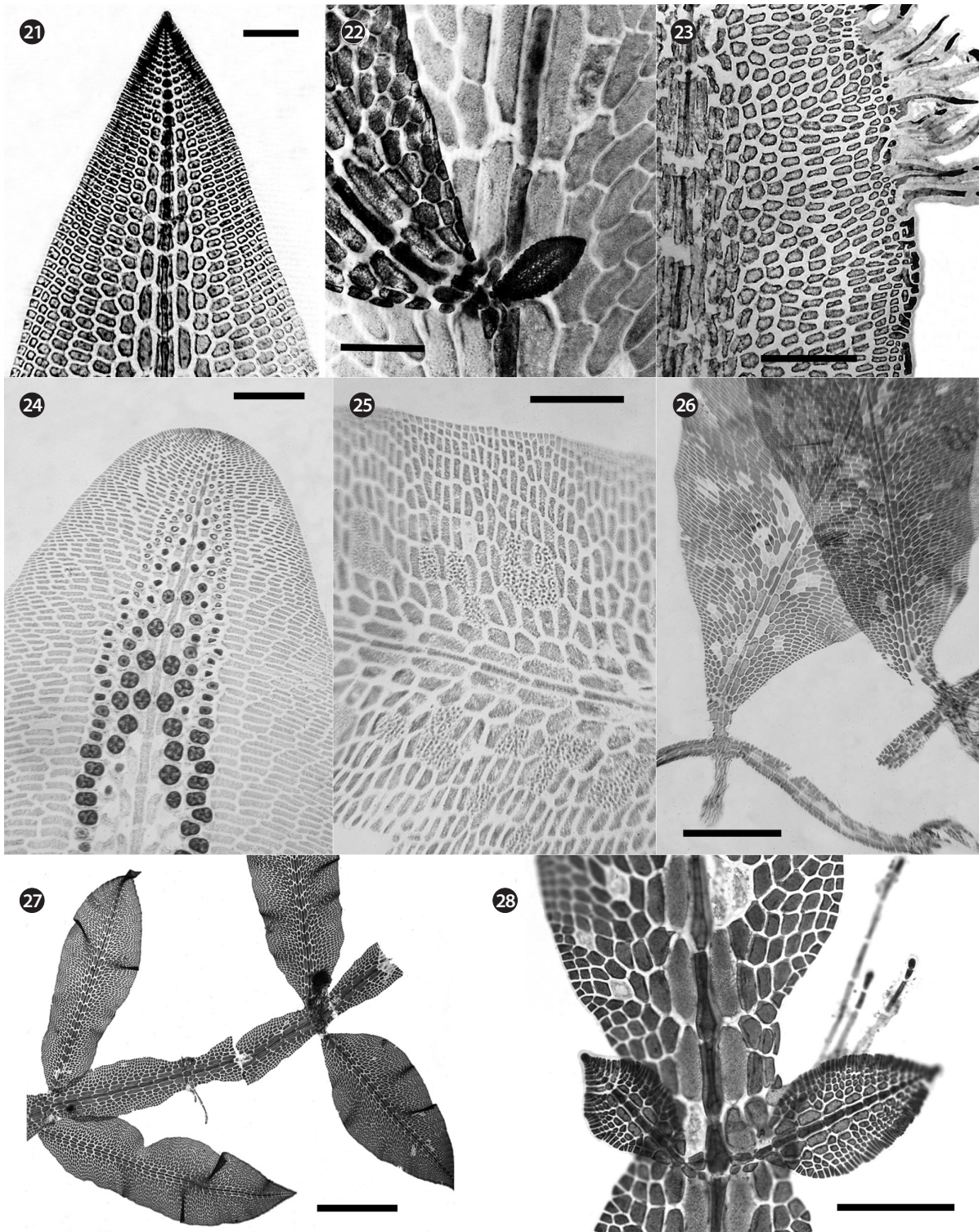
*Searlesia* was established by Schneider and Eiseman (1979) as a new genus based on *Membranoptera subtropica* de-





**Figs 13-20.** **Figs 13 & 15.** *Hypoglossum tenuifolium*. [Puerto Rico, D. Ballantine 1518]. **Fig. 13.** Apex with Type-2 pattern. **Fig. 15.** Blade with scattered spermatangial sori. **Figs 14, 16 & 17.** *Hypoglossum anomalum*. [Puerto Rico, D. Ballantine 1782]. **Fig. 14.** Pair of branch primordial emerging between midline and blade margin. **Fig. 16.** Apex with Type-1 pattern. **Fig. 17.** Blade with tetrasporangial sorus. **Figs 18-20.** *Hypoglossum hypoglossoides*. **Fig. 18.** Apex with Type-1 pattern. [North Carolina, USA, C. Schneider 862]. **Figs 19 & 20.** [Bermuda, C. Schneider 09-30-26]. **Fig. 19.** Branch arising from axial row. **Fig. 20.** Blade with tetrasporangial sorus. Scale bars represent: Figs 13, 16 & 18, 40  $\mu\text{m}$ ; Figs 14 & 15, 100  $\mu\text{m}$ ; Fig. 17, 150  $\mu\text{m}$ ; Figs 19 & 20, 200  $\mu\text{m}$ .





**Figs 21-28.** **Figs 21 & 22.** *Hypoglossum simulans*. **Fig. 21.** Apex with Type-2 pattern. **Fig. 22.** Endogenous origin of branch from basal segment of parent blade. [Guadeloupe, D. Ballantine 2490] (after Wynne et al. 1989). **Fig. 23.** *H. barbatum*. Multicellular rhizoids produced from blade margin. [Bermuda, C. Schneider & R. Searles 85-20-20] (after Schneider 2000). **Figs 24 & 25.** *H. subsimplex*. **Fig. 24.** Blade with tetrasporangial sorus. **Fig. 25.** Blade with spermatangial sori. [Type collection, Florida, USA, M. Wynne 9959]. **Fig. 26.** *H. rhizophorum*. Habit. Isotype specimen [Puerto Rico, D. Ballantine 1750]. **Figs 27 & 28.** *H. caloglossoides*. **Fig. 27.** Habit. **Fig. 28.** Constricted node with a pair of branches arising endogenously from central axial row. [Bermuda, C. Schneider & C. Lane 01-22-14] (after Schneider 2004). Scale bars represent: Figs 21 & 23-25, 50  $\mu$ m; Figs 22, 26 & 28, 100  $\mu$ m; Fig. 27, 0.5 mm.

scribed from deep water off North Carolina, USA (Schneider 1974). But Yoshida and Mikami (1991) later presented reasons to merge *Searlesia* within *Polyneura* while still recognizing *P. subtropica* (C. W. Schneid.) T. Yoshida et Mikami. *Cyclospora*, a name based on a type species from Florida and treated by Taylor (1960) as a genus of Delesseriaceae, was merged by Wynne (1985) into *Carpoblepharis* in the Ceramiaceae.

#### Examples of new species based on western Atlantic types:

Rhodophyta: *Aglaothamnion flexibile* (Aponte and Ballantine 1995), *Antithamnionella bermudica* (Schneider and Searles 1997), *Antithamnionella schneideri* (Athanasiadis 1996), *Branchioglossum minutum* (Schneider in Schneider and Searles 1975), *B. prostratum* (Schneider 1974), *Calliblepharis occidentalis* (Joly et al. 1965), *Callithamniella silvae* (Searles and Schneider 1989), *Centroceras internitens* (Gallagher and Humm 1983), *Ceramium bisporum* (Ballantine 1990), *Ceramium fujianum* (Barros-Barreto et al. 2006), *Ceramium itonoi* (Ardre 1987), *Ceramium reptans* (Cho and Fredericq 2006), *Chamaebotrys prolifera* (Ballantine et al. 2010), *Champia feldmannii* (Diaz-Piferrer 1977), *Champia harveyana* (Ballantine and Lozada-Troche 2008), *Champia minuscula* (Joly and Ugadim in Joly et al. 1966), *Champia puertoricensis* (Lozada-Troche and Ballantine 2010), *Champia taironensis* (Bula-Meyer 1997), *Chondria platyramea* (Joly and Ugadim in Joly et al. 1966), *Chrysymenia littleriana* and *C. nodulosa* (Norris and Ballantine 1995), *Chylocladia schneideri* (Ballantine 2004), *Cirrucarpus carolinensis* (Hansen 1977), *Corallina panizzoi* (Schnetter and Richter 1979), *Craspedocarpus humilis* (Schneider 1988), *Crouania elisiae* (Schneider 2004), *Crouania mayae* (Mateo-Cid et al. 2002), *Cryptonemia delicatula* (Joly and Cordeiro in Joly et al. 1966), *Cryptonemia flabellifolia* (Pinheiro-Joventino and Oliveira 1977), *Dasya abbottina* (Ballantine and Aponte 2004) (Fig. 38), *Dasya haitiana* (Fredericq and Norris 1986), *Dasya magnei* (Ballantine 2000), *Dasysiphonia concinna* and *D. doliformis* (Schneider 1989), *Diplothamnion jolyi* (van den Hoek 1978), *D. tetrastichum* (Joly and Yamaguishi in Joly et al. 1966), *Halymenia clathrata* (Oliveira et al. 1976), *Haralda tenuis* (Oliveira 1969), *Helminthocladia andersonii* (Searles and Lewis 1983), *Helminthora anomala* (Vélez and Vega 2005) (Fig. 44), *Herposiphonia xaymaca* (Chapman 1963), *Hypnea volubilis* (Schneider and Searles 1976), *Jania prolifera* (Joly in Joly et al. 1966), *Jania sanctae-marthae* (Schnetter 1972), *Kallymenia westii* (Ganesan 1976) (Fig. 39), *Lejoliea exposita* (Searles and Schneider 1989), *Ligora tsengii* (Huisman and Wynne 1999) (Fig. 45), *Lithophyllum depressum* (Villas-Boas et al. 2009), *Mazoyerella kraftii* (Bucher and Norris 1995), *Naccaria antillana* (Taylor 1971), *Nemalion cari-cariense* (Schnetter 1972), *Nitophyllum adhaerens* (Wynne 1997), *Perikladosporon abaxiale* (Ballantine and Aponte 2005), *Periphykon delesserioides* (Joly et al. 1967), *Petroglossum undulatum* (Schneider and Searles 1976), *Platysiphonia caribaea* (Ballantine and Wynne 1985), *Polysiphonia boldii* (Wynne and Edwards 1970), *P. plectocarpa* (Schneider and Searles 1998), *Porphyra acanthophora* and *P. spiralis* (Oliveira and Coll 1975), *Porphyra pujalsii* and *P. rizzinii* (Coll and Oliveira 1976), *Ramicrusta textilis* (Pueschel and Saunders 2009), *Schimmelmannia venezuelensis* (Ballantine et al. 2003) (Fig. 40), *Seirospora viridis* (Aponte and Ballantine 1995), *Stichothamnion antillarum* (Vroman 1967), *Titanophora submarina* (Bucher and Norris 1992), *Woelkerlingia sterreri* (Schneider and Wynne 2009)

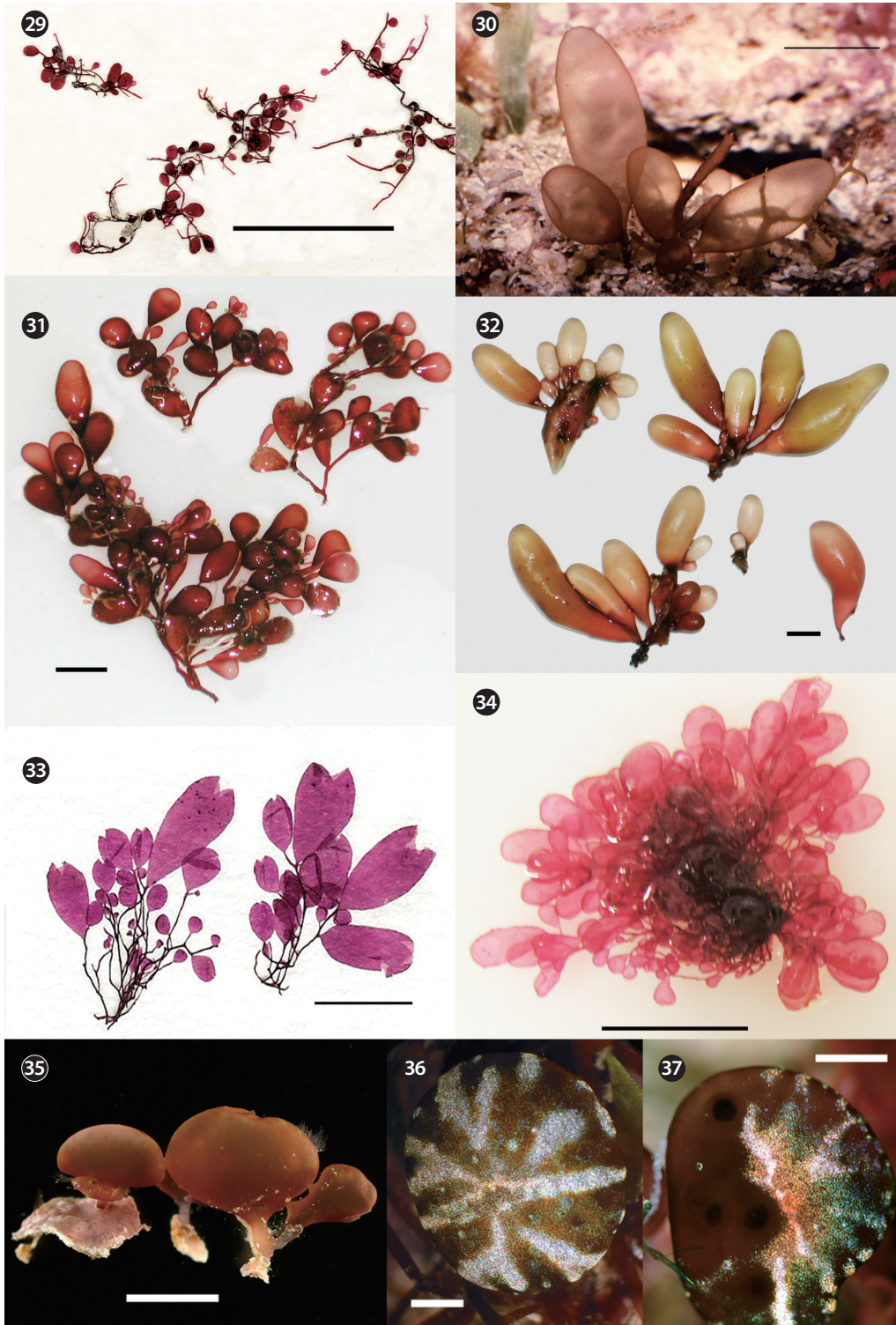
Heterokontophyta: *Dictyopteris jolyana* (Oliveira and Furtado 1978), *Dictyota caribaea*, *D. guajirae* and *D. humifusa* (Hörnig et al. 1992), *Dictyota pulchella* (Hörnig and Schnetter 1988), *Laminaria abyssalis* and *L. brasiliensis* (Joly and Oliveira 1967), *Onslowia bahamensis* (Henry 1987), *Padina boergesenii* (Allender and Kraft 1983) (Fig. 46), *P. profunda* (Earle 1969), *Sargassum mathiesonii* (Kilar 1992), *Sargassum pusillum* (Taylor 1975), *Sargassum wolfii* (Earle 1969), *Stictyosiphon lutarius* (Taylor 1974), *Syringoderma floridana* (Henry 1984)

Chlorophyta: *Acetabularia myriospora* (Joly et al. 1965), *Avrainvillea cyathiformis* (Ballantine and Aponte 2003), *Boodleopsis vaucherioidea* (Calderón-Sáenz and Schnetter 1989), *Bryopsis halliae* (Taylor 1962a) (Fig. 48), *Caulerpa kempfii* (Joly and Pereira 1975), *Codium carolinianum* (Searles 1972), *Halimeda goreau* (Taylor 1962d) (Fig. 49), *Halimeda pumila* (Verbruggen et al. 2007b), *Ostreobium constrictum* (Lukas 1974), *Pseudocodium floridanum* (Dawes and Mathieson 1972), *Rhipidosiphon floridensis* (Littler and Littler 1990a), *Trichosolen molassensis* (Bucher and Norris in Bucher et al. 1990)

A number of genera have received monographic treatments, have otherwise relatively large levels of attention, or have had new species assigned. These genera are listed below with citations of their treatments:

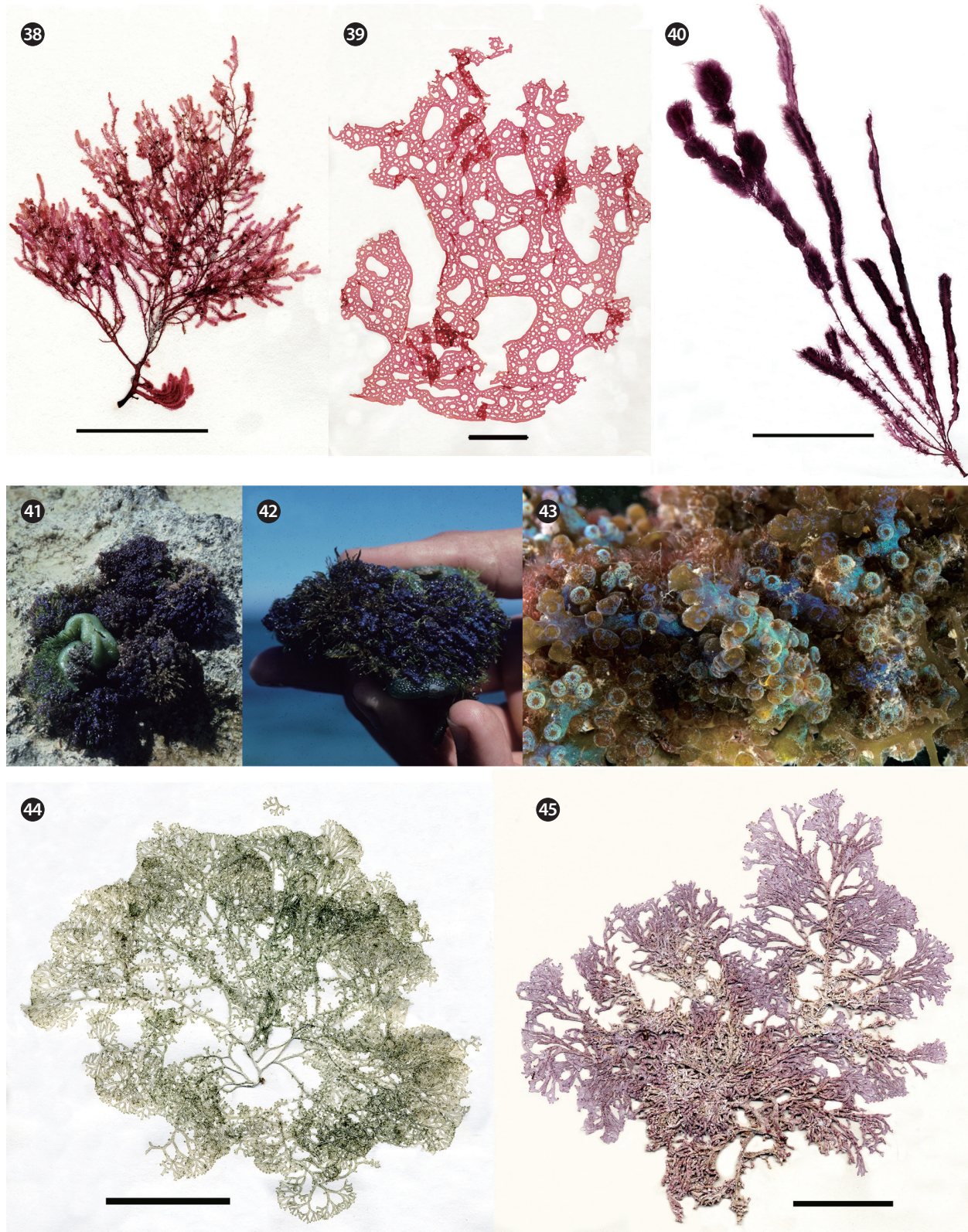
*Aglaothamnion* and *Callithamnion*: Aponte and Ballantine (1990, 1995); Aponte et al. (1994, 1997); Brasileiro et al. (2009); Cordeiro-Marino (1978); Dixon and Price (1981); Guimarães (2006); L'Hardy-Halos and Rueness (1990); Maggs et al. (1991); Rueness and L'Hardy-Halos (1991); Rueness and Rueness (1980); Schneider (1980); Searles (1981); Wynne (2005)





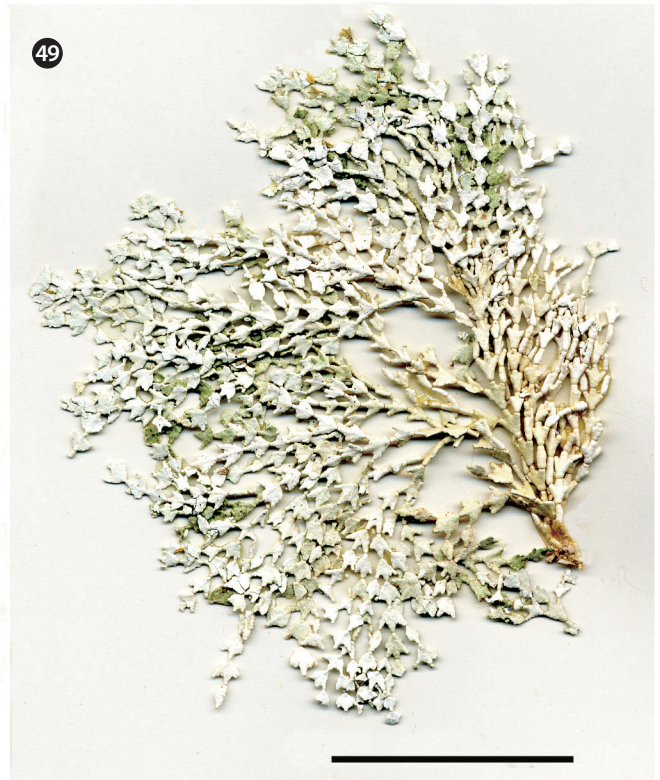
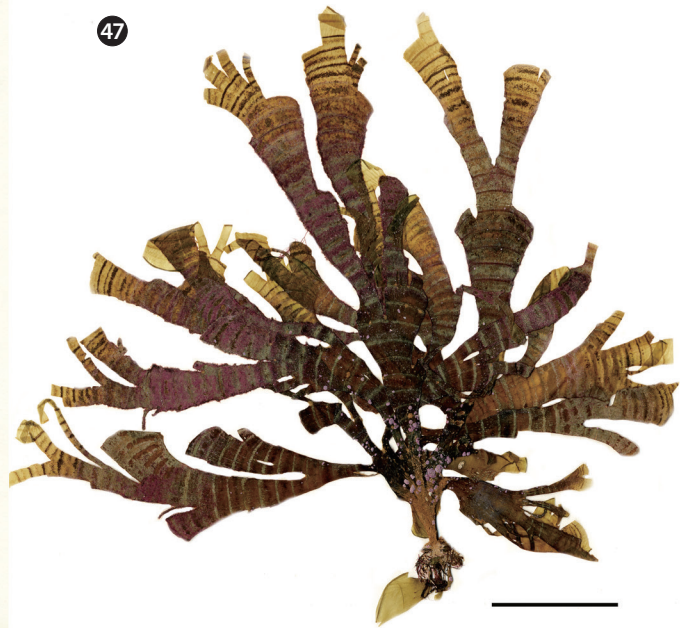
**Figs 29-37.** **Fig. 29.** *Botryocladia spinulifera*. [U.S. Virgin Is., N. Ogden N-490]. Habit, pressed specimen. **Fig. 30.** *B. wynnei*. [Puerto Rico, Ballantine]. *In situ* specimens. **Fig. 31.** *B. bermudana*. [Bermuda, C. Schneider & C. Lane 02-11-1]. Aquarium specimens. **Fig. 32.** *B. flookii*. [Bermuda, C. Schneider & C. Lane 03-16-9]. Habit of living specimens. **Figs 33 & 34.** *B. exquisita*. [Bermuda, C. Schneider & C. Lane 08-16-2]. **Fig. 33.** Habit of an isotype. **Fig. 34.** Habit of type collection. **Figs 35-37.** *B. iridescens*. **Fig. 35.** Wet habit of Holotype. [Puerto Rico, D. Ballantine 6342]. **Fig. 36.** Vesicle showing a stellate pattern of iridescence. [Puerto Rico, D. Ballantine 6307]. **Fig. 37.** Vesicle showing a spotted pattern of iridescence. [Puerto Rico, D. Ballantine 6376] (Figs 35-37 after Ballantine and Ruiz 2008). Scale bars represent: Fig. 29, 3 cm; Fig. 30, 4 mm; Figs 31-33, 1 cm; Fig. 34, 2 cm; Fig. 35, 5 mm; Fig. 36, 1 mm; Fig. 37, 2 mm.





**Figs 38-45.** **Fig. 38.** *Dasya abbottiana*. Habit. [Isotype, Puerto Rico, H. Ruiz & D. Ballantine 6100]. **Fig. 39.** *Kallymenia westii*. Habit. [Venezuela, Wynne 7862]. **Fig. 40.** *Schimmelmannia venezuelana*. Habit. [Holotype, Venezuela, M. García 48]. **Figs 41-43.** *Palisada iridescens* (M. J. Wynne & D. L. Ballant.) K.W. Nam. **Figs 41 & 42.** Type collection, Guadeloupe, Ballantine & Wynne. **Fig. 43.** Puerto Rico, H. Rúa & D. Ballantine 8263. **Fig. 44.** *Helminthora anomala*. Habit. [Holotype, Puerto Rico, R. Vega & C. García 4202]. **Fig. 45.** *Liagora tsengii*. Habit. [Holotype, St. Kitts, M. Edlund & M. Wynne 10663]. Scale bars represent: Figs 38, 44 & 45, 3 cm; Figs 39 & 40, 6 cm.





**Figs 46-49.** **Fig. 46.** *Padina boergesenii*. Habit. [Guadeloupe, M. Wynne 8320]. **Fig. 47.** *Padina glabra*. Habit. [Texas, USA, M. Wynne 2588]. **Fig. 48.** *Bryopsis halliae*. Habit. [Isotype, Florida, USA, Mrs. G. Hall]. **Fig. 49.** *Halimeda goreauii*. Habit. [Isotype, Jamaica, T. Goreau & J. Lang]. Scale bars represent: 3 cm.

*Dudresnaya*: Eiseman and Norris (1981); Searles (1983); Searles and Ballantine (1986)  
*Gracilaria*: Bodard (1965); Gurgel and Fredericq (2004); Gurgel et al. (2004a, 2004b, 2004c, 2008); Hommersand and Freshwater (2009); McLachlan (1979); Pinheiro and Joly (1966); Plastino and Oliveira (1997, 2002)  
*Gracilariopsis*: Bird and Oliveira (1986); Fredericq and Hommersand (1989); Gurgel et al. (2003a, 2003b)  
*Peyssonnelia*: Ballantine and Aponte (2005); Ballantine and Ruiz (2005, 2006, 2007, 2010, 2011); Boudouresque and Denizot (1975); Joly et al. (1968); Marcot-Coqueugniot (1988); Schneider and Reading (1987); Yoneshigue (1984)  
*Anadyomene*: Joly and Pereira (1973); Joly and Oliveira (1968); Littler and Littler (1991)  
*Avrainvillea*: Joly et al. (1966); Littler and Littler (1992)  
*Cladophora*: Norris and Olsen (1991); van den Hoek (1969, 1982); van den Hoek and Searles (1988)  
*Halimeda*: Ballantine (1982); Colinvaux and Graham (1964); Dawes (1980); Dawes and Humm (1969); Goreau and Graham (1967); Guimaraes et al. (2009a, 2009b); Hillis (1959); Hillis-Colinvaux (1980); Taylor (1962d); Verbruggen et al. (2005); Verbruggen et al. (2007b)  
*Udotea*: Littler and Littler (1990b)  
*Verdigellas*: Ballantine and Aponte (1996); Ballantine and Norris (1994)

### Examples of new records for the western Atlantic:

The red alga *Reticulocaulis mucosissimus* I. A. Abbott was described from 8-10 m depths off Hawaii by Abbott (1985), and so the discovery of its presence from Espírito Santo State, Brazil, by Guimaraes and Amado-Filho (2009) is an interesting range extension. Earlier, it has been found to occur in Oman (Schils et al. 2003) and the Canary Islands (Afonso-Carrillo et al. 2006). A comparable case is the report by Ballantine et al. (2009) of *Predaea laciniosa* from Puerto Rico, representing the first record of this species from the Atlantic Ocean. This species was described by Kraft (1984) with a type locality of Heron Island, Great Barrier Reef, Australia.

*Laurencia pygmaea* Weber Bosse, a species with a type locality of Diego Garcia Atoll in the Indian Ocean (Weber van Bosse 1913) and previously unknown for the Atlantic Ocean, was reported from Brazil (Oliveira and Ugadim 1974) and Venezuela (Rodriguez de Rios and Lobo 1984). But several workers (Jaasund 1970, Furnari and Cormaci 1990, Wynne 1995) later treated it as conspecific with *L. decumbens* Kütz., a species first described from New Caledonia (Kützing 1863).

The range of *Padina glabra* Gaillard, described from Dakar, Senegal, West Africa (Gaillard 1966), has been extended to the east coast of Florida (Wynne and De Clerck 1999) and to Texas (Wynne 2009a) (Fig. 47). It is a distinctive species because of the absence of hairs.

Van den Hoek and Rios (1972) reported the occurrence of *Willeella ordinata* Borgesen, a green algal species first described from Gujarat, India, to be present in Venezuela. Van den Hoek (1982) later reduced *Willeella* to the status of a section within *Cladophora*. Although some authors (e.g., Silva et al. 1996) continued to recognize *Willeella* as a genus, according to Wysor and Kooistra (2003) their separation as two discrete genera is not supported by molecular data.

Ballantine et al. (2009) reported the occurrence of *Boergesenia forbesii* (Harv.) Feldmann from Puerto Rico, representing the first record of this monotypic genus from the Atlantic. It is well known from various locations in the tropical Indo-Pacific, including Australia, southern Japan, China, Sri-Lanka, and the east coast of Africa.

*Caulerpa ollivieri*, a species that was described from the Mediterranean coast of France (Dostál 1929), was reported to occur in two deep-water sites in the Gulf of Mexico (Hine and Humm 1971). But more recently its invasive spread in the Bahamas has been reported by Lapointe et al. (2005), despite the fact that in its home range it has been listed as an endangered species by the Berne Convention (the European Centre for Nature Conservation).

*Halimeda cuneata* K. Hering in Krauss, a species with a type locality of Natal Bay, South Africa (Krauss 1846), was reported for the first time to occur in the Atlantic by its record from Brazil by Bandeira-Pedrosa et al. (2004). The authors expressed the opinion that earlier collections had likely been mistaken for *H. discoidea* or *H. tuna* or else had been called "*Halimeda* sp." *Halimeda pygmaea*, a species originally described from Astrolabe Reef, Fiji, South Pacific (Verbruggen et al. 2007b), was reported from Cuba by Guimaraes et al. (2009b), representing its first record in the Atlantic.

*Rhipilia tomentosa* Kütz. was the only species in the genus included in Taylor's (1960) flora. Later, Joly and Sazima (1971) reported from Brazil *R. orientalis* A. Gepp et E. Gepp, described from the Malay Archipelago, Indonesia (Gepp and Gepp 1911) and *R. diaphana* W. R. Taylor, described from Bikini Atoll, Northern Marshall Islands (Taylor 1950). *Rhipilia fungiformis* was a newly described species from Itaparica Island, Bahia, Brazil by Joly and Ugadim (Joly et al. 1965).



Oliveira (1977) pointed out that *R. tenaculosa* was described by Gepp and Gepp (1911) from deep water off Barra Grande, near Pernambuco, Brazil. But it was missed by Taylor (1960).

### Examples of clarifications of uncertain taxa:

An ongoing task of workers in systematic phycology is the need to be aware of possible misunderstood taxa or of misinterpretations of the type specimens of taxa. One example is the work by Allender and Kraft (1983), who observed that the holotype of *Padina gymnospora* (Kütz.) Sond. [= *Zonaria gymnospora* Kütz.] was up to 8 or 9 cell layers in thickness and thus did not correspond to the contemporary idea of that species. They relegated *P. vickersiae* to the status as a taxonomic synonym of *P. gymnospora* and described the new species *P. boergesenii* (Fig. 46) to accommodate the *Padina* that had fit the wrong concept of *P. gymnospora*, a blade of 2-3 cell layers in thickness.

Similarly, De Clerck and Coppejans (1997) found the Holotype of *Dictyota crispata* J. V. Lamour. in the Lamouroux Herbarium in Caen, France, and recognized that concepts of that species and *D. bartayresiana* Kütz. had been confused by many workers. What Vickers (1908) and others had depicted as "*Dictyota bartayresiana*" agreed well with the type of *D. crispata*. This meant that *D. neglecta* Hörnig et Schnetter (Hörnig et al. 1992), which had been described to include the specimens of *D. bartayresiana* auct. non Vicker, becomes a superfluous name for *D. bartayresiana*.

An example of the consolidation of many (five) names into one recognized taxon is shown by Fiore's (1977) work, in which he used laboratory-based culturing studies to demonstrate that a heteromorphic life history was occurring in a brown alga occurring along the east coast of North America and the Gulf of Mexico. The larger sporophytic phase, a cylinder up to 12 cm tall and with parenchymatous construction, had gone under the name *Stictyosiphon subsimplex* Holden, and the smaller gametophytic phase, of 1-3 mm-tall tufts with sympodial growth, trichothallic hair formation, and lateral dimorphic plurilocular gametangia, had gone under the name *Farlowiella onusta* (Kütz.) Kornmann and several taxonomic synonyms. Fiore provided persuasive evidence that a single taxon was involved. Earlier, Fiore (1975) had proposed the new name *Hummia* to replace the illegitimate name *Farlowiella* Kornmann in Kuckuck (1956).

*Bakothamnion* was described by van den Hoek (1978), based on *B. curassavicum* Hoek from Curaçao, Netherland Antilles. But according to Young (1981), that species is conspecific with *Balliella pseudocorticata* (E. Y. Dawson) D. N. Young. The genus *Balliella* Itono et Tanaka (1973) was based on the type species *B. crouanioides* (Itono) Itono et T. Tanaka from Mage Island, southern Japan.

*Dasya brasiliensis* was described from Praia da Figueira, São Francisco, State of São Paulo, Brazil, by Oliveira and Braga (1971). But more recently Ritzmann et al. (2007) treated it as conspecific with the widely occurring *D. rigidula* (Kütz.) Ardiss.

An example of generic clarification was that on the *Pseudobryopsis* / *Trichosolen* complex by Henne and Schnetter (1999). *Bryopsis duchassaingii* J. Agardh was included by Taylor (1960), but later Taylor (1962a, 1962c) recognized that *B. duchassaingii* belongs to the genus *Trichosolen* (Montagne 1861). Taylor (1962c) treated *Pseudobryopsis* (Berthold in Oltmanns 1904) as congeneric with *Trichosolen*, both genera having specialized gametangia, a feature distinguishing them from *Bryopsis*. But Henne and Schnetter (1999) presented evidence for the generic distinction of *Trichosolen* and *Pseudobryopsis* on the basis of differences in the nature of the gametangia and the chloroplasts.

In the category of clarifications are those species that were long thought to be the same as familiar European species because of their remarkable superficial similarity. But modern tools of gene-sequencing have sometimes revealed instances of cryptic speciation, where the European-based types are genetically distinct from their western Atlantic counterpart. For example, De Clerck et al. (2005) have shown that *Grateloupia filicina*, despite its many reports from the western Atlantic and elsewhere, is limited to the Mediterranean basin. Some work will be required to determine if one or another of the names thought to be taxonomic synonyms might be available to serve for the western Atlantic material.

According to Stuercke and Freshwater (2008) the names *Polysiphonia denudata* (Dillwyn) Harv. and *P. stricta* (Dillwyn) Grev. [= *P. urceolata* (Dillwyn) Grev.] that have been applied to collections from the western Atlantic do not correspond to these European-based species on the basis of genes examined. In a later paper, Stuercke and Freshwater (2010) described two new species from the western Atlantic. *Polysiphonia schneideri*, with a type locality of Wrightsville Beach, New Hanover County, North Carolina, USA, was used for material that had previously been mis-identified as *P. denudata*. They did not recognize *P. denudata* as present in the western Atlantic. The second new species, *P. kapraunii*, with a type locality of Masonboro Inlet, New Hanover County, North Carolina, USA, was used for some (but not all) material

from the western Atlantic that had previously been mis-identified as *P. stricta* (and its taxonomic synonym *P. urceolata*). They did recognize *P. stricta* as also present in the western Atlantic.

Several species of *Gracilaria* that were recognized as present in the western Atlantic by Taylor (1960) have subsequently been shown to have more restricted distributions. Plastino and Oliveira (1996) stated that *G. verrucosa* (Huds.) Papenf. does not occur in Brazil and probably not in the Caribbean. Later, Irvine and Steentoft (1995) presented arguments for the rejection of the basionym *Fucus verrucosus* Huds. *Gracilariopsis longissima* (S. G. Gmel.) M. Steentoft, L. M. Irvine et W. F. Farnham (1995) became the correct name for what had been called *Gracilaria verrucosa* in Europe, but other species of *Gracilariopsis* have been shown to be the correct names for related species in the western Atlantic, such as *Gracilariopsis carolinensis* (Gurgel et al. 2003b) as well as *G. silvana*, *G. hommersandii*, and *G. cata-luziana* (Gurgel et al. 2003a). *Gracilaria tenuifrons*, a species described from Algoas in northeastern Brazil by Bird and Oliveira (1986), was later transferred to *Gracilariopsis* by Fredericq and Hommersand (1989).

Some of Taylor's (1960) concept of "*Gracilaria foliifera*" was treated in part as *G. intermedia* by Gurgel et al. (2004b) and in part as the new species *G. isabellana* by Gurgel et al. (2004a). Wynne (2005) pointed out that the neglected but valid name *G. patens* P. Crouan et H. Crouan needs to be reinstated for Caribbean *Gracilaria* with thalli consisting of a spreading clump of mostly dichotomously branched, compressed axes and for which Taylor (1960) applied the incorrect name "*G. foliifera*." Taylor's (1960) "*Gracilaria debilis*," a species with a type locality of Al Mukha, Yemen, in the Red Sea, is thought not to be present in the western Atlantic (Bird et al. 1986) and is now known as *Hydropuntia cornea* (J. Agardh) M. J. Wynne (Wynne 1989). Another species that had been placed in *Gracilaria* by Taylor (1960), *G. crassissima*, is now assigned to *Hydropuntia*, and several other species have been either newly described or have been assigned to *Hydropuntia* (Rodríguez de Rios 1986, Wynne 1989, Gurgel and Fredericq 2004). Bird et al. (1986) offered reasons to dismiss the name *G. wrightii* (Turner) J. Agardh from the flora. Oliveira et al. (1983) presented evidence to merge *Gracilaria ferox* J. Agardh, a species that had been recognized by Taylor (1960), within *G. cervicornis* (Turner) J. Agardh.

Taylor (1960) recognized *Halymenia floresii* (Clemente) C. Agardh, the European-based generitype, as occurring in the western Atlantic. In addition, there was the morphologically similar *H. pseudofloresii* Collins et M. Howe, with Walsingham Pond, Bermuda, as type locality. Schneider et al. (2010) described the great morphological variability in specimens of *H. pseudofloresii* from Bermuda, and they also provided molecular evidence that *H. pseudofloresii* is sister to *H. floresii*. Using barcoding sequences, Schneider et al. (2010) demonstrated that the narrow to extremely broad specimens all represented a single taxon in the islands and removed *H. floresii* from the flora. Furthermore, they questioned all other records of *H. floresii* from the western Atlantic until they are positively compared with the European generitype.

According to Wang et al. (2005), molecular data do not support the monophyly of such putatively pantropical species as *Dichotomaria marginata* (J. Ellis et Sol.) Lam., *D. obtusata* (J. Ellis et Sol.) Lam., and *Galaxaura rugosa* (J. Ellis et Sol.) J. V. Lamour. Cryptic speciation may be present in those species.

Another example of cryptic species being recognized and separated is the work by Ballantine and Lozada-Troche (2008), who showed that *Champia harveyana*, their new species from Puerto Rico, can be distinguished from the similar *C. salicornioides* Harv. The two species are sister taxa in the same clade but differ on internal morphologies, different branching patterns, and also on sequence analyses of two genes. Similarly, *Champia puertoricensis* was recognized as a new species by Lozada-Troche and Ballantine (2010) from sympatrically occurring *C. parvula* (C. Agardh) Harv. on the basis of differences in branching pattern, origin of branches, monoecious or dioecious conditions, and gene sequences. Bula-Meyer (1997) was able to separate out *Champia taironensis*, a new species from the Caribbean coast of Colombia, from two other flattened species of the genus, *C. compressa* Harv. and *C. vieillardii* Kütz., by a suite of differences.

*Dictyota dichotoma* (Hudson) J. V. Lamour. had been long reported from the American Atlantic, but Schnetter et al. (1987) were able to demonstrate that the American plants were not interfertile with European plants, and they had different chromosome numbers. So the name *D. menstrualis* (Hoyt) Schnetter, Hörnig et Weber-Peukert was applied to the American counterpart.

*Dictyota pfaffii* was described from Punta Brava, Isla Grande, on the Caribbean coast of Colombia by Schnetter (1972). But De Clerck (2003) and Wysor and De Clerck (2003) have presented arguments to regard *D. pfaffii* as conspecific with *D. friabilis* Setch., a species described from Tahiti (Setchell 1926).

Some instances of invasive species have been reported. *Gracilaria vermiculophylla* (Ohmi) Papenf., with a type locality of Akkeshi Bay, Hokkaido, Japan, has earlier been reported from many sites on the coast of Atlantic Europe, where it is regarded as an invasive (Rueness 2005). It was first reported from the east coast of North America from Virginia (Thom-

sen et al. 2006) and next from North Carolina (Freshwater et al. 2006). *Porphyra yezoensis* Ueda, a species being commercially cultivated in Japan and China (Tseng 1981), has been reported to have spread into the North Atlantic, including New England, USA (Neefus et al. 2008). Molecular evidence of its presence on the coast of Texas has also been reported (Wynne 2009b). There was a deliberate introduction of the carrageenophytes *Eucheuma denticulatum* (Burman) Collins et Herv. and *Kappaphycus alvarezii* (Doty) P. C. Silva into waters of Venezuela and Brazil for commercial utilization. The invasive potential of *K. alvarezii* in waters off the state of Rio de Janeiro was considered remote (Castelar et al. 2009).

All of these various circumstances of the past half century, including expanded exploration into previously uncharted areas and using SCUBA for collecting at greater depths, the increase in the number of phycologists in countries of the tropical and subtropical western Atlantic Ocean, and the use of new technologies of gene-sequencing combined with phylogenetic analyses, have resulted in significant changes in the number of taxa of benthic marine algae. This fact applies to all hierarchical ranks, from infraspecific taxa and species to orders and classes. Many examples can be cited of the recognition that the application of names of species based on European types for western Atlantic material has not been correct. Also, the utilization of molecular systematics has often led to the appreciation of cryptic speciation and that what had been regarded to be widely occurring species actually represent species complexes. It is anticipated that these trends will continue as will be expected the introduction of invasive species into this flora.

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