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Benthic-epiphytic dinoflagellates from the northern portion of the Mesoamerican Reef System

Abstract: In 2010, we surveyed 42 sampling locations at 11 sites along the Mexican part of the Mesoamerican Reef System, including eight protected natural areas of the coastal state of Quintana Roo, to determine the richness of benthic-epiphytic dinoflagellates in the area. At each site, the host macroalgae of the genera *Dictyota*, *Halimeda*, *Laurencia*, *Sargassum*, and *Styopodium* were manually collected. A total of 383 samples were analyzed microscopically using transmitted light, epifluorescence with calcofluor staining, and scanning electron microscopy. A total of 24 dinoflagellate species distributed among the genera *Amphidinium*, *Bysmatrum*, *Coolia*, *Gambierdiscus*, *Ostreopsis*, *Prorocentrum*, *Plagiodinium*, and *Sinophysis* were identified. *Prorocentrum* is the most diverse genus in the benthic-epiphytic environment with 13 species. This work also includes 15 new records of species from the Mexican Caribbean.

Keywords: benthic microalgae; Ciguatera; coral reefs; Dinophyceae; epiphytic dinoflagellates; Mexican Caribbean.

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Introduction

Dinoflagellates are an important component of the benthic microflora in tropical coral reef systems, either as part of the flora in sandy substrates (Faust 2000) or associated as epiphytic species on macroalgae and seagrasses (Cruz-Rivera and Villareal 2006, Okolodkov et al. 2007). Some species of benthic-epiphytic dinoflagellates produce toxins that may affect public health through the consumption of marine products (especially carnivorous fishes) contaminated with these compounds.

Gambierdiscus toxicus (Adachi and Fukuyo 1979) has long been considered as the main source of ciguatoxins (CTXs) and, hence, the main cause of ciguatera fish poisoning (CFP). This species has been the subject of many studies pertaining to its systematics, toxicity, and ecological behavior (Yasumoto et al. 1977, 1980). Several new species of *Gambierdiscus* have been described, including some that are toxic (Litaker et al. 2010, Rhodes et al. 2014), raising the question whether all the previous reports of toxicity in *Gambierdiscus* strains should really be referred to *G. toxicus*. Later, Yasumoto et al. (1987) demonstrated that the benthic genera *Amphidinium*, *Coolia*, *Ostreopsis*, and *Prorocentrum* also contain species that produce toxins. From these studies, several so-called ciguatoxic areas have been identified in the West Pacific, along Australian coasts, and in the Caribbean Sea (Besada et al. 1982, Tindall et al. 1984, Ballantine et al. 1988). In recent years, research on benthic dinoflagellates has spread to higher latitudes in light of new reports of the presence of *Ostreopsis* species (Chateau-Degat et al. 2005, Monti et al. 2007, Shears and Ross 2009, Granéli et al. 2010). Moreover, new species of benthic dinoflagellates have been recently described (Fraga et al. 2008, Litaker et al. 2009, Chui-Pin et al. 2010, Fraga et al. 2011). In the Mesoamerican Reef System off Belize, several toxic species of the genera *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum* were described by Faust (1990, 1993a,b, 1994, 1995a,b, 1997, 1999), as well as the non-toxic genus *Plagiodinium* (Faust and Balech 1993).

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Q1: Please supply the full postal address for second affiliation of "Francisco Valadez".

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There is limited knowledge on the benthic dinoflagellates from the coasts of Mexico. *Gambierdiscus toxicus*, *Prorocentrum lima*, *P. belizeanum*, and *Sinophysis canaliculata* have been reported for the Mexican Pacific (Okolodkov and Gárate-Lizárraga 2006). In the Veracruz coral reef system, located in the Gulf of Mexico, Okolodkov et al. (2007) reported 17 taxa, including *G. toxicus*, *P. lima*, *P. concavum*, and *A. carterae*. On the Caribbean coasts of Quintana Roo, the presence of the toxic species *G. belizeanus* Faust, *G. yasumotoi* Holmes, *P. belizeanum*, *P. lima*, *P. mexicanum* Osorio-Tafall, and *P. ruetzlerianum* Faust has been reported (Almazán-Becerril 2000, Hernández-Becerril and Almazán-Becerril 2004).

The study of benthic dinoflagellates is important not only because some species produce toxins, but also because of their role in microbial food webs and in maintaining reef ecosystem functions, among others. However, these ecological aspects are virtually unknown.

Currently, the deterioration of reef systems caused by the loss of coral has led to a predominance of macroalgae.

This process has been called phase shift (Hoegh-Guldberg et al. 2007). A possible consequence of this phenomenon is the increase in the absolute number of epiphytic dinoflagellates, including toxic species, and therefore, a possible increase in the incidence of CFP events. Therefore, the first step in a series of long- and medium-term studies on the ecology of toxic dinoflagellates and ciguatera is to assess species richness in an area. In this regard, the present study was conducted with that particular aim in mind.

Materials and methods

The Mexican Caribbean includes the coastal fringe of the Mexican state of Quintana Roo (Figure 1). This zone hosts the northern portion of the Mesoamerican Reef System, from the southern border of Mexico and Belize to Cape Catoche at the northeast of the Yucatan Peninsula. The area includes eight natural protected areas.

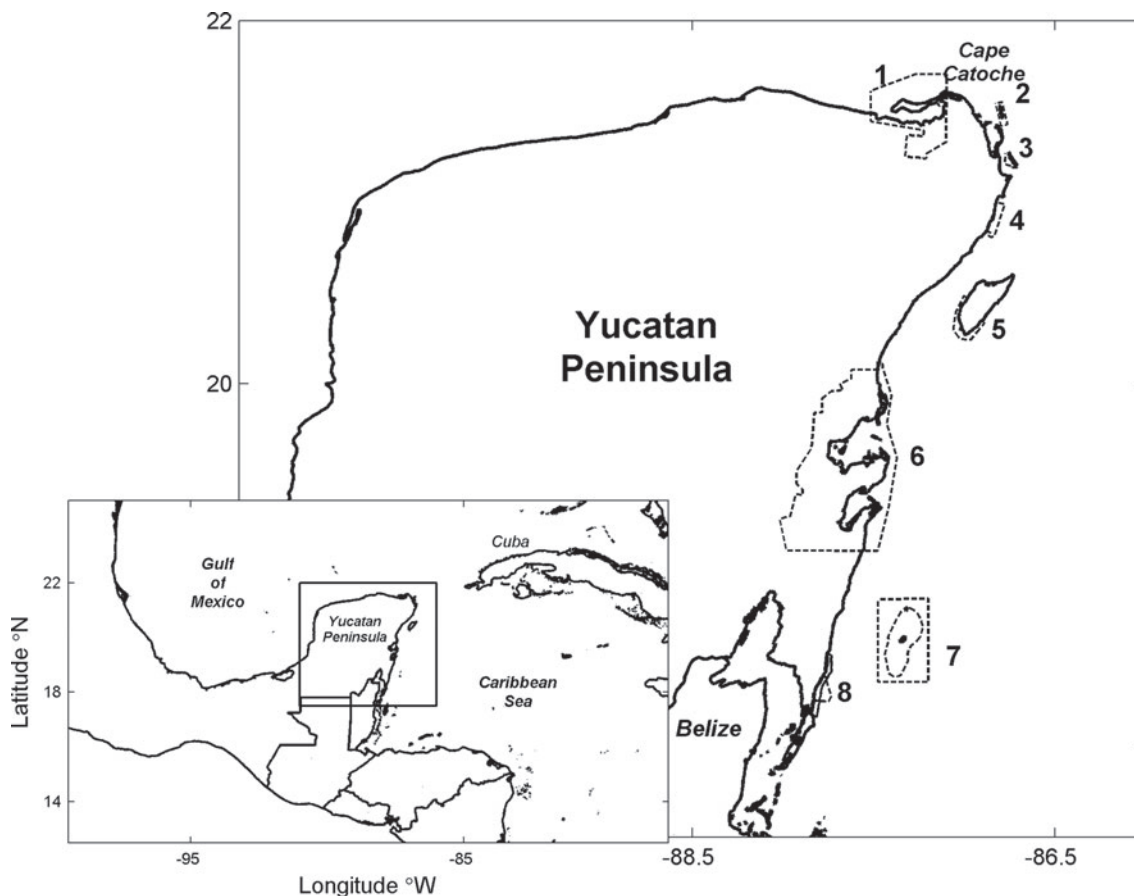


Figure 1: Sampling points in the Mexican Caribbean coast (black circles). At each point, three to five sites were selected for macroalgal collection. Protected Natural Areas are indicated by broken lines: (1) Yum Balam, (2) Isla Contoy, (3) Isla Mujeres, (4) Puerto Morelos Reefs, (5) Cozumel Reefs, (6) Sian ka'an Biosphere Reserve, (7) Chinchorro Bank Biosphere Reserve, (8) Xcalak Reefs.

A total of 383 macroalgae were sampled in 11 localities along the coast of Quintana Roo from April to October 2010. At each locality, macroalgal specimens were collected by hand and stored in Ziploc® bags. During sampling, an effort was made to cover the full variety of macroalgae. The macroalgae collected were fixed with 4% formaldehyde in seawater to preserve both the substrate and the epiphytic cells. Dinoflagellates were detached from the macroalgae by vigorous shaking and then transferred to a plastic bottle.

Observations and measurements of morphological features were mainly performed on cleaned dinoflagellates using light microscopy. Specimens were cleaned of salty water and preservatives by at least 10 rinse steps. Each step involved centrifugation at 2500 rpm. After careful withdrawal of the supernatant, the pellet was re-suspended in deionized water. This material was used to prepare fresh, semi-permanent, and permanent slides mounted with both glycerine jelly and Naphrax (Reid 1978).

Differential interference contrast and epifluorescence microscopy were performed using an Axio Imager A2 microscope system, and digitally photographed with an AxioCam ICc 1 camera and Axiovision software (Carl Zeiss AG, Oberkochen, Germany). Following the calcofluor method of Fritz and Triemer (1985), plate tabulation was examined under fluorescence microscopy using Fluorescent Brightener 28 (Sigma-Aldrich Co., St. Louis, MO, USA). For cell dissection, the cells were submerged in a drop of sodium hypochlorite solution and squashed by gently pressing the cover slip (Fraga et al. 2011). For SEM analyses, cells were washed in deionized water and dehydrated in an ethanol series (30%, 50%, 70%, 80%, 95%, and 100%). The supernatant was removed after the sedimentation/centrifugation of the cells. Samples were CO₂-critical-point dried, coated with a layer of gold, and examined on a Jeol JSM 6360LV electron microscope.

For taxonomic identification, the specialized literature was consulted, including the recent papers of Faust and Steidinger (1998), Selina and Hoppenrath (2004), Mohammad-Noor et al. (2007), Litaker et al. (2009), Fraga et al. (2011), and Hoppenrath et al. (2013). The classification scheme proposed by Fensome et al. (1993) was followed.

The frequency of each species in the samples was expressed as the percentage of occurrence (the ratio of the number of samples where the species was present to the total number of samples, multiplied by 100).

Results

A total of 24 species of epiphytic dinoflagellates belonging to five orders and seven families were identified (Table 1,

Figures 2–62). Fifteen of the species are new records for the Mexican Caribbean (marked with asterisks in Table 1): eight species of *Prorocentrum*, three of *Bysmatrum*, two of *Sinophysis*, and one each of *Ostreopsis* and *Plagiodinium*. *Prorocentrum* was the genus with the highest number of species recorded (Figures 2–22).

Prorocentrum lima (Figures 2–3, 61) and *P. hoffmannianum* (Figures 4–5, 53–54) were the species most frequently recorded – they were present in 100% and 93% of the samples, respectively. *Prorocentrum belizeanum* (Figures 10–11), *P. emarginatum* (Figures 8–9), *P. rathymum* (Figures 6–7), and *Prorocentrum* sp. (Figure 58) were also well represented, with their occurrence in the samples ranging from 29% to 60%. *Prorocentrum concavum* (Figure 13), *P. arenarium* (Figures 14–15), and *P. maculosum* (Figures 16–17) showed lower occurrences (5%–14%). *Prorocentrum caribbaeum* (Figure 18) and *P. fukuyoi* (Figure 12) were found in only a few samples. Finally, *P. gracile* (Figure 22) and *P. lebourae* (Figure 20) have been reported to be mainly planktonic forms; hence, their presence on the macroalgae could be incidental.

Two *Ostreopsis* species were identified: *O. heptagona* (Figures 32–35, 41–42) and *O. siamensis* (Figures 36–38, 43–44). The occurrences of both ranged from 1% to 9% of the total number of samples.

Gambierdiscus cf. *carolinianus* (Figures 45–46, 50–51) was widely recorded in all sites and was observed in 50% of the samples. *Gambierdiscus belizeanus* and *G. yasumotoi* were reported in previous surveys in the zone (Hernández-Becerril and Almazán-Becerril 2004), but were not collected in this study.

Coolia cf. *tropicalis* (Figures 39–40) was widely distributed and well represented in the area, with its frequency near 55%. The potentially toxic species *Amphidinium* cf. *carterae* (Figures 23 and 47) was also observed in nearly 50% of the samples. The monotypic genus *Plagiodinium* (*P. belizeanum*) was observed only in some sites from Holbox (2.5% of the samples, Figure 24). The non-toxic genera *Bysmatrum* and *Sinophysis* contributed five species: *B. caponii* (Figures 25–26, 48), *B. granulosum* (Figure 27), *B. subsalsum* (Figure 28), *S. canaliculata* (Figures 31, 49, and 62), and *S. microcephalus* (Figures 29–30). *Bysmatrum caponii* was abundant in several sites and occurred in 38% of the samples, whereas the occurrence of *S. canaliculata* was 31%.

Discussion

The Mesoamerican Reef System is a region where toxic and non-toxic benthic dinoflagellates species have been widely

Table 1: Taxonomic list of benthic and epiphytic dinoflagellate species recorded from the Mexican Caribbean coast in 2010.

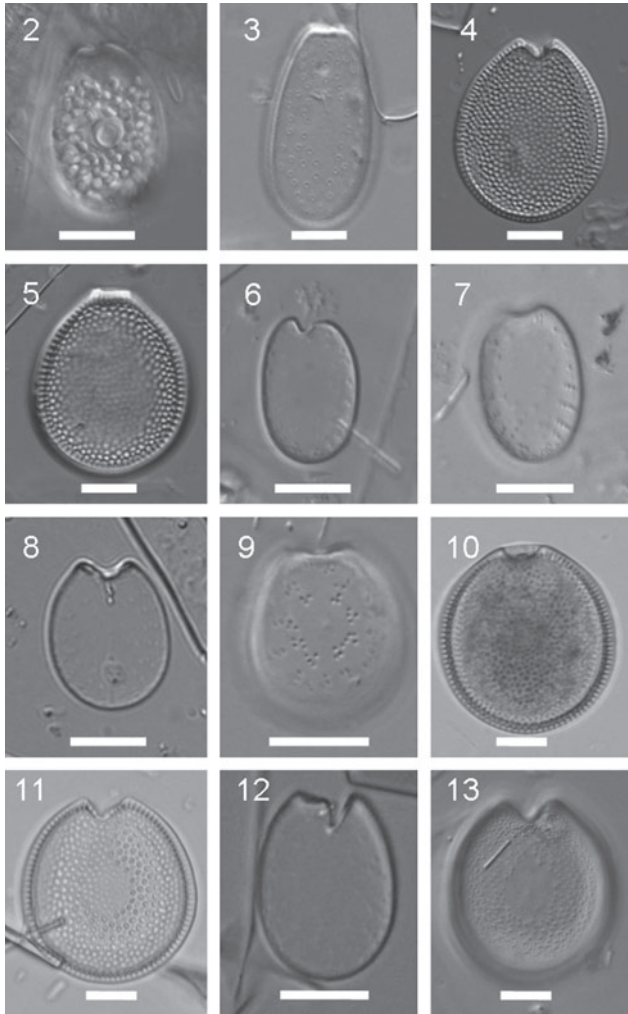
Order	Gymnodiniales Lemmermann 1910	
	Family	Gymnodiniaceae Lankester 1885
		Genus <i>Amphidinium</i> Claparède et Lachmann 1859
		<i>A. cf. carterae</i> Hulburt 1957
Order	Dinophysiales Lindemann 1928	
	Family	Dinophysiaceae Stein 1883
		Genus <i>Sinophysis</i> Nie et Wang 1944
		<i>S. canaliculata</i> Quod, Ten-Hage, Turquet, Mascarell et Couté 1999*
		<i>S. microcephalus</i> Nie et Wang 1944*
Order	Gonyaulacales Haeckel 1894	
	Family	Goniodomataceae Lindemann 1928
		Genus <i>Gambierdiscus</i> Adachi et Fukuyo 1979
		<i>G. cf. carolinianus</i> Litaker, Vandersea, Faust, Kibler, Holland et Tester 2009
	Family	Ostreopsidaceae Lindemann 1928
		Genus <i>Coolia</i> Meunier 1919
		<i>C. cf. tropicalis</i> Faust 1995
	Family	Ostreopsidaceae Lindemann 1928
		Genus <i>Ostreopsis</i> Schmidt 1901
		<i>O. heptagona</i> Norris, Bomber et Balech 1985
		<i>O. siamensis</i> Schmidt 1901*
Order	Peridinales Haeckel 1894	
	Family	Peridiniaceae Ehrenberg 1830
		Genus <i>Bysmatrum</i> Faust et Steidinger 1998
		<i>B. caponii</i> (Horiguchi et Pienaar) Faust et Steidinger 1998*
		<i>B. granulatum</i> Ten-Hage, Quod, Turquet et Couté 2001*
		<i>B. subsalsum</i> (Ostenfeld) Faust et Steidinger 1998*
Order	Prorocentrales Lemmermann 1910	
	Family	Prorocentraceae Stein 1883
		Genus <i>Plagiodinium</i> Faust et Balech 1993
		<i>P. belizeanum</i> Faust et Balech 1993*
		Genus <i>Prorocentrum</i> Ehrenberg 1834
		<i>P. arenarium</i> Faust 1994*
		<i>P. belizeanum</i> Faust 1993
		<i>P. caribbaeum</i> Faust 1993*
		<i>P. concavum</i> Fukuyo 1981*
		<i>P. emarginatum</i> Fukuyo 1981*
		<i>P. fukuyoi</i> Murray et Nagahama 2007*
		<i>P. gracile</i> Schütt 1895*
		<i>P. hoffmannianum</i> Faust 1990
		<i>P. lebourae</i> Schiller 1928*
		<i>P. lima</i> (Ehrenberg) Dodge 1975
		<i>P. maculosum</i> Faust 1993*
		<i>P. rathymum</i> Loeblich, Shirley et Schmidt 1979
		<i>Prorocentrum</i> sp.

The new species records for this region are marked with an asterisk (*).

recorded and new species described. However, the results of the present study indicate lower species richness than in recent reports for the genera *Ostreopsis* (Rhodes 2011), *Gambierdiscus* (Litaker et al. 2010), and *Prorocentrum* (Faust 1990, 1993a,b, 1997, Faust et al. 2008) in the Caribbean region. The same is true for the non-toxic genera *Bysmatrum* and *Sinophysis*, which together contributed a total of only five species, although the total number of

species reported for each genus is higher (Hoppenrath 2000, Selina and Hoppenrath 2004, Murray et al. 2006). Similarly, only one *Amphidinium* species was observed, although this genus is recognized for its high species diversity (Jørgensen et al. 2004). Finally, the monotypic genus *Plagiodinium* was also found infrequently in the samples.

The main cause of this apparently low species diversity could be the sampling strategy, which was directed only to



Figures 2–13: Light microscopy of *Prorocentrum* species. (2–3) *Prorocentrum lima* from Isla Mujeres, right valve. (4–5) *Prorocentrum hoffmannianum* from Puerto Morelos, right and left valves, respectively. (6–7) *Prorocentrum rathymum* from Akumal, right valve. (8–9) *Prorocentrum emarginatum* from Tulum, right and left valves, respectively. (10–11) *Prorocentrum belizeanum* from Isla Mujeres, right valve. (12) *Prorocentrum fukuyoi* from Puerto Morelos, right valve. (13) *Prorocentrum concavum* from Isla Mujeres, right valve. Scale bars=20 μm .

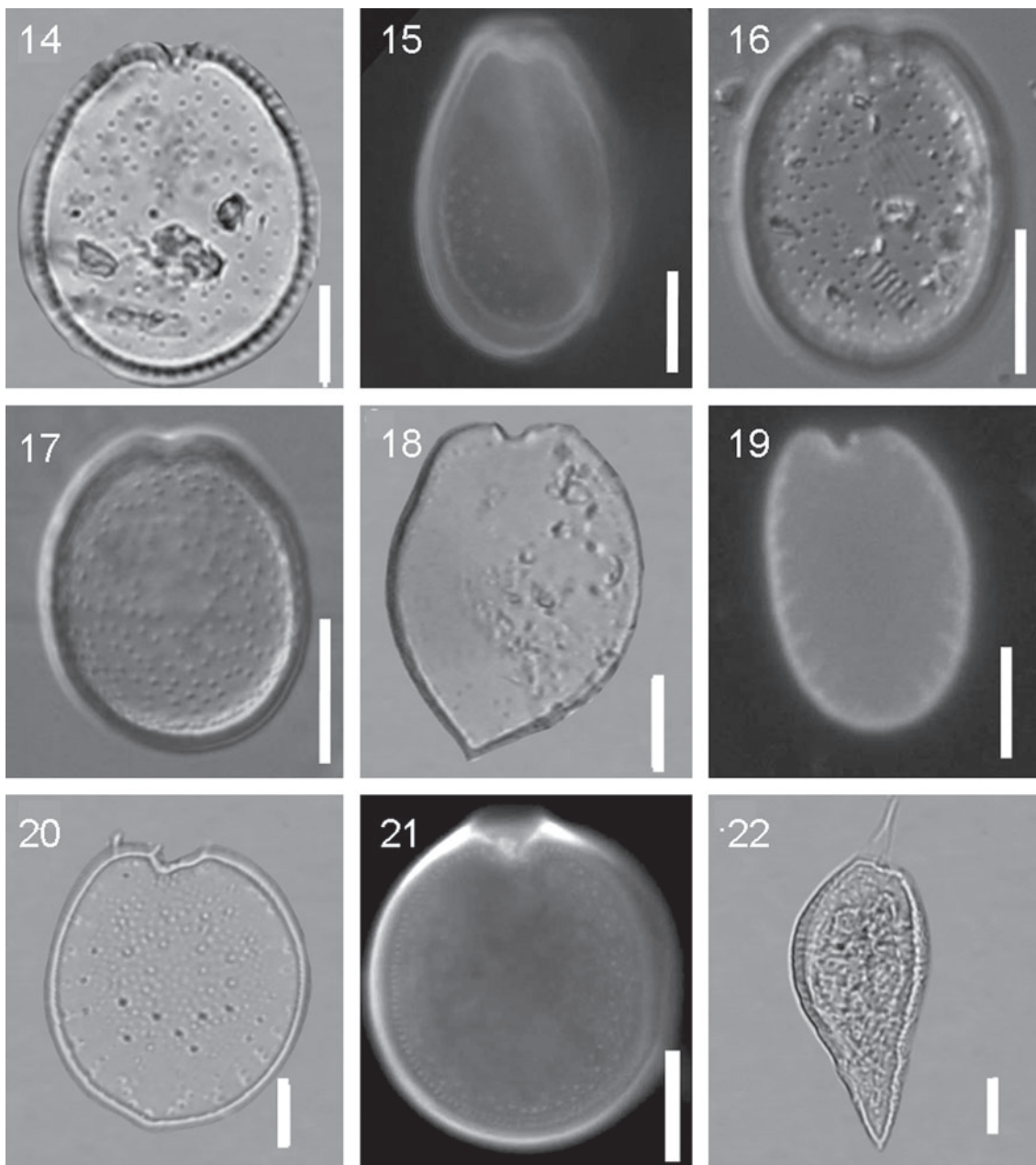
macroalgae, or environmental variables associated with the sampling site. It is also possible that there was a mismatch between the seasonality of the demographic peak of some populations and the time of sampling. Another possible reason for the apparently low diversity of species may be the methodology used in the present study. Taxonomic studies of unarmored dinoflagellates (e.g., *Amphidinium* cells), or the so-called thin-walled dinoflagellates, require mainly living samples and specific techniques and protocols for their study because of their delicate form

(Escobar-Morales and Hernández-Becerril 2015), so these approaches should be considered for future surveys in the area. It should be mentioned that the epiphytic life form is only a fraction of the benthic habitat, and that new species and genera have been found in the interstitial spaces of sandy substrata (Murray and Patterson 2002, Tamura and Horiguchi 2005). These sand-dwelling dinoflagellates are heterogeneously distributed in this environment, some inhabiting the intertidal habitat and others the subtidal domain. For example, Saburova et al. (2009) found a great diversity of dinoflagellates in the intertidal sediments of Kuwait, including several species of *Amphidinium* and other uncommon genera, such as *Herdmania* Dodge, *Roscoffia* Balech, or *Thecadinium* Kofoid et Skogsberg. In addition, Faust (1993a,b, 1995a) found many new sand-dwelling species of *Prorocentrum*, *Gambierdiscus*, and *Coolia* in shallow, subtidal, semi-enclosed environments in the Belize reef.

Although the richness of benthic-epiphytic dinoflagellates in the present study was lower than that reported in the region as a whole, our results are similar to the findings from other areas of the Caribbean (Morton and Faust 1997, Delgado et al. 2006), and to other studies where only macroalgae were sampled in Malaysia (Mohammad-Noor et al. 2007), the Western Indian Ocean (Hansen et al. 2001), Hawaii (Parsons and Preskitt 2007), and the Mediterranean Sea (Vila et al. 2001).

The dynamics of dinoflagellate populations are probably linked to the seasonal variability of sea surface temperature and nutrient availability (Vila et al. 2001, Delgado et al. 2006, Okolodkov et al. 2007, Parsons and Preskitt 2007). Although there are no reliable data on the seasonality of nutrient concentrations in the Mexican Caribbean, some evidence suggests a positive correlation of this variable with the rainy season (August to October) because of the increase in groundwater discharge (the main source of inorganic nitrogen) to the coast. In contrast, the warmest period in the zone occurs from May to July. This indicates an uncoupling between the maximum concentration of nutrients and the maximum sea surface temperature, with the consequence that the peaks of dinoflagellates abundance are unpredictable.

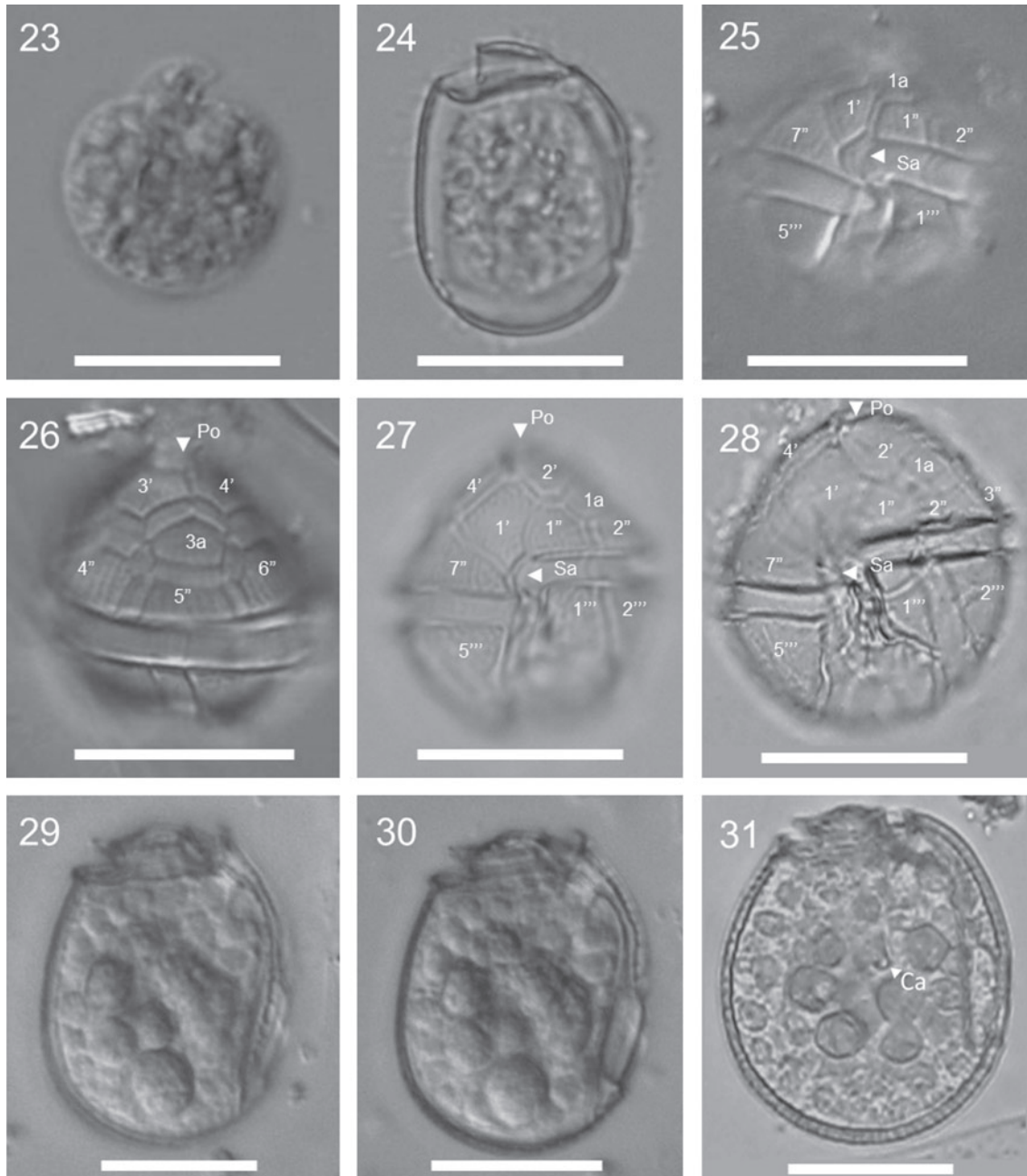
Prorocentrum dominance is a consistent feature of the benthic assemblages at tropical latitudes (Hansen et al. 2001, Mohammad-Noor et al. 2007, Parsons and Preskitt 2007), where *P. lima* has been recognized as the most abundant species. Indeed, *P. lima* is considered a widely-distributed species frequently observed in planktonic samples (Steidinger and Tangen 1997). *Prorocentrum belizeanum* (Figure 21) and *P. hoffmannianum* are two closely related species having a distinctive



Figures 14–22: Light microscopy and fluorescence micrographs of *Prorocentrum* species. (14) *Prorocentrum arenarium* from Akumal, right valve. (15) Same as Figure 14, but stained with calcofluor. (16–17) *Prorocentrum maculosum* from Isla Mujeres, right valve. (18) *Prorocentrum caribbaeum* from Isla Mujeres, right valve. (19) *Prorocentrum rathymum* from Puerto Morelos, right valve stained with calcofluor. (20) *Prorocentrum lebourae* from Isla Contoy, right valve. (21) *Prorocentrum belizeanum* from Cozumel, right valve stained with calcofluor. (22) *Prorocentrum gracile* from Sian ka'an, right valve. Scale bars: 14, 15, 19, 20, and 22=10 μm ; 16, 17, 20, and 21=20 μm .

feature – the deeply areolated pattern of their thecae – although they are easily identified by their size and cell shape (Figures 53–54). These are the largest *Prorocentrum* species reported in the region. Therefore, it is logical to suppose that their size and high occurrence should be indicative of their importance in the benthic

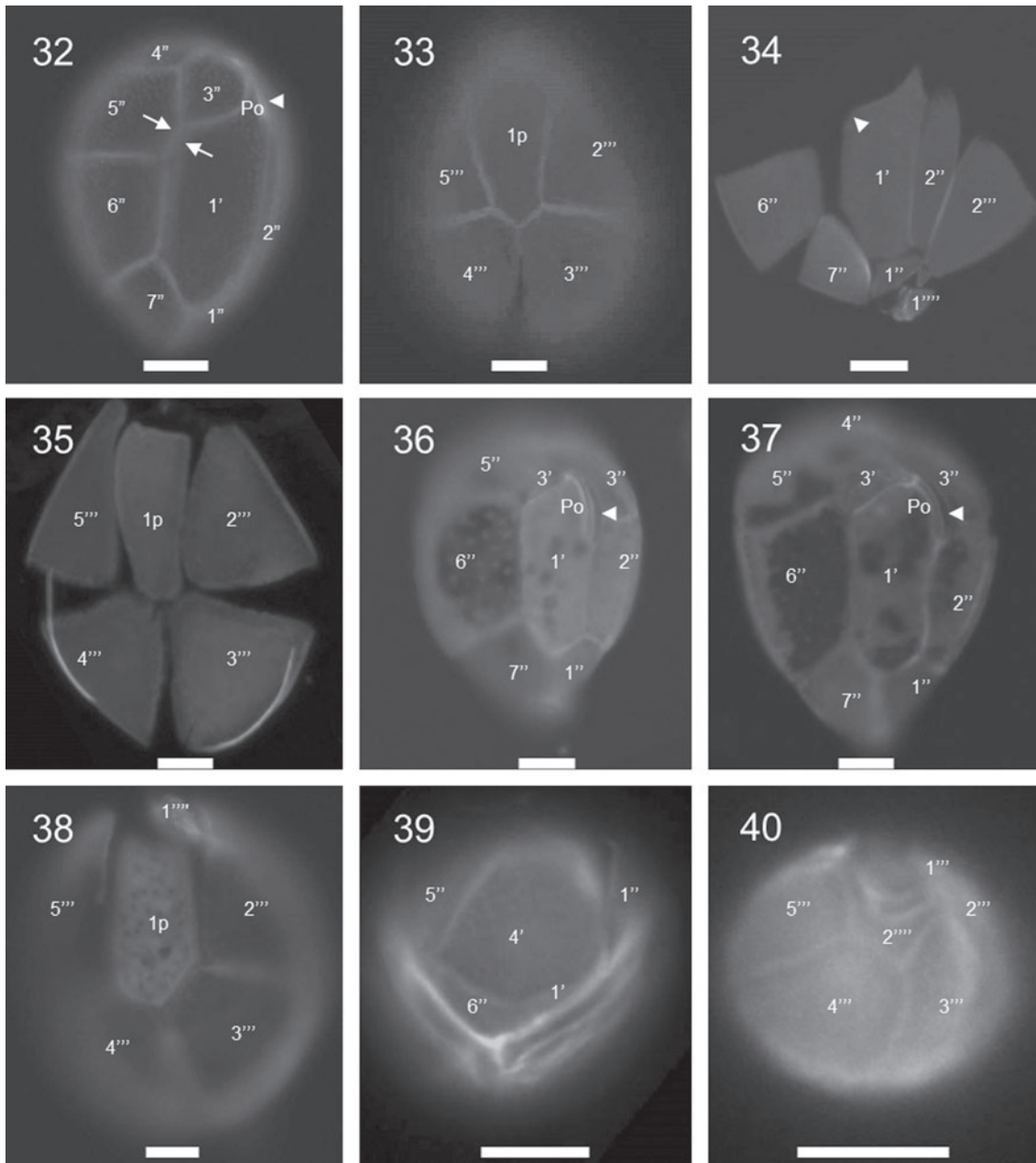
microhabitat given that they have been observed in the Caribbean (Faust 1990, 1993a), Hawaii (Parsons and Preskitt 2007), and the west Indian Ocean (Hansen et al. 2001). *Prorocentrum emarginatum* (Figure 57) and *P. rathymum* (Figures 55–56) are two small species that were widely distributed and found frequently in our



Figures 23–31: Light microscopy of *Amphidinium*, *Bysmatrum*, *Plagiodinium*, and *Sinophysis*. (23) *Amphidinium* cf. *carterae* from Isla Contoy, ventral view. (24) *Plagiodinium belizeanum* from Sian ka'an, lateral view. (25–26) *Bysmatrum caponii* from Tulum, ventral and dorsal views, respectively. (27) *Bysmatrum granulatum* from Tulum, ventral view. (28) *Bysmatrum subsalsum* from Isla Mujeres, ventral view. (29–30) *Sinophysis microcephalus* from Isla Mujeres, right lateral view. (31) *Sinophysis canaliculata* from Puerto Morelos, right lateral view. Ca, canicula; Po, pore; Sa, anterior sulcal plate. Scale bars=20 μm .

samples. Apparently, their distribution is wider than that of *P. belizeanum* and *P. hoffmannianum*, and they are also present in the Mediterranean Sea (Vila et al. 2001). Except for *P. caribbaeum* (Figure 18), *P. lebourae* (Figure 20), *P. fukuyoi* (Figures 59–60), and *P. gracile* (Figure 22), the

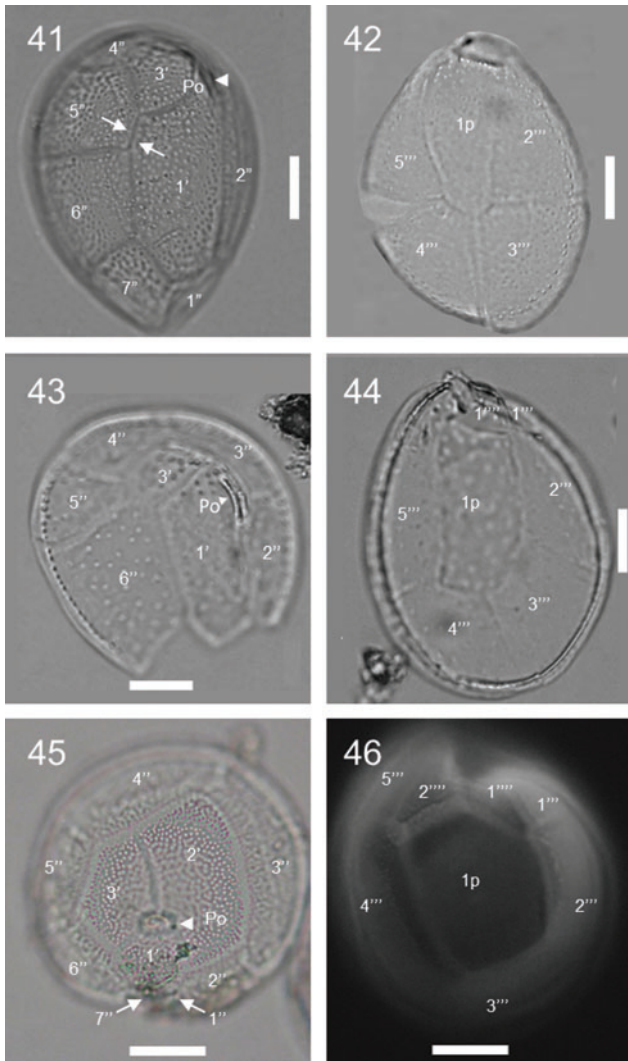
remaining *Prorocentrum* species are reported to be toxic (Faust and Gullede 2002) and, given their high abundance and presence along the entire Caribbean coast of Mexico, they could be responsible for an important fraction of toxin production.



Figures 32–40: *Coolia* and *Ostreopsis*, cells stained with calcofluor. (32–35) *Ostreopsis heptagona* from Yum Balam (Holbox), arrows indicate the point where the 1' and 5' plates touch: (32) apical view; (33) antapical view; (34) squashed epitheca; (35) squashed hypotheca. (36–38) *Ostreopsis siamensis* from Puerto Morelos: (36) apical view; (37) apical view with different focus; (38) antapical view. (39–40) *Coolia tropicalis* from Isla Mujeres: (39) apical view; (40) antapical view. Po, pore. Scale bars=20 μ m.

Members of *Gambierdiscus* are probably the main species responsible for ciguatera. In fact, *G. toxicus* has been traditionally associated with CFP. Several studies have reported the presence of *G. toxicus* in the Caribbean region (Parsons et al. 2012). *Gambierdiscus toxicus* was previously reported in the study area by Hernández-Becerril and Almazán-Becerril (2004).

However, Litaker et al. (2009, 2010) did not find *G. toxicus* in the Caribbean. This inconsistency could be attributed to the differences in the methodology: whereas previous studies were performed only with morphological observations, Litaker et al. (2009) described the new species *G. carolinianus* (among three other species) on the basis of both morphological differences and phylogenetic analyses



Figures 41–46: Light microscopy and fluorescence micrographs of *Gambierdiscus* and *Ostreopsis*. (41–42) *Ostreopsis heptagona* from Xcalak: (41) apical view, arrows indicate the point where the 1' and 5' plate touch; (42) antapical view. (43–44) *Ostreopsis siamensis* from Isla Contoy, epitheca, with the pores scattered around the surface. (45–46) *Gambierdiscus* cf. *carolinianus* from Tulum: (45) apical view; (46) antapical view after staining with calcofluor. Po, pore. Scale bars=20 μ m.

using molecular tools. Our observations suggest that *G.* cf. *carolinianus* (Figures 45–46) has been misidentified as *G. toxicus* because of the pattern and shape of the plates 2' and 1p. *Gambierdiscus carolinianus* presents a broad 2''' plate and a hatchet-shaped 2' plate (Figures 50–51).

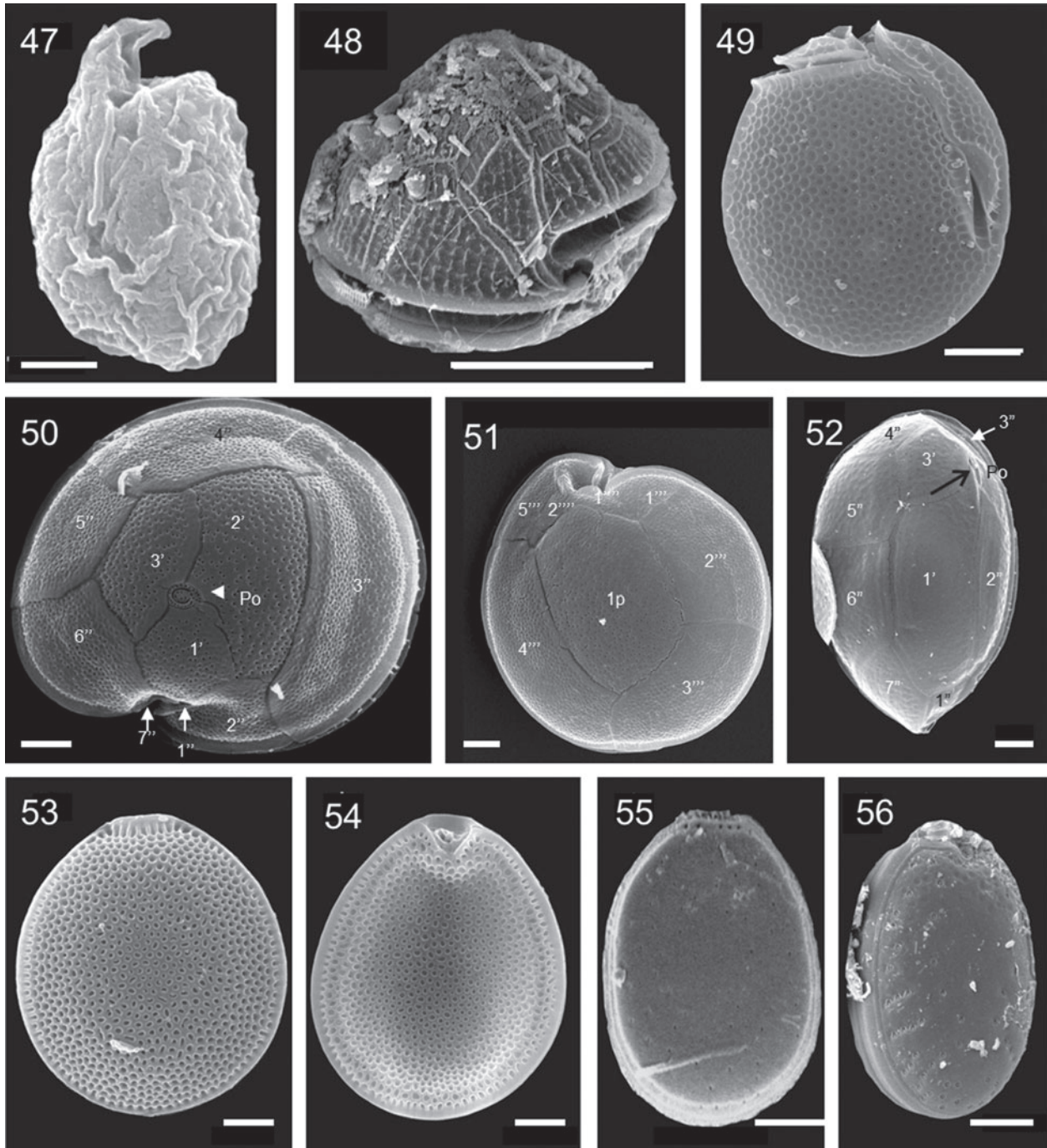
It is possible that more *Gambierdiscus* species inhabit the zone because previous works have documented the presence of *G. belizeanum*, *G. yasumotoi*, and *G. carolinianus* (= *G. toxicus*; Hernández-Becerril and Almazán-Becerril 2004). Moreover, Litaker et al. (2010)

and Tester et al. (2013) reported the occurrence of the recently described *G. carolinianus* and *G. carpenteri* Kibler, Litaker, Faust, Holland, Vandersea *et* Tester in the northern coastal zone of Quintana Roo. This information suggests that at least 30% of the *Gambierdiscus* species are present on the Mexican Caribbean coasts.

The genus *Ostreopsis* has received special attention worldwide because of its apparent spread to temperate latitudes (Monti et al. 2007, Shears and Ross 2009). In the Mediterranean Sea, *O. ovata* Fukuyo and *O. siamensis* (Figures 36–38) have been associated with massive blooms, toxin production, respiratory problems in humans, and sea urchin mortalities (Aligizaki and Nikolaidis 2006, Ciminiello et al. 2006). In New Zealand, large numbers of *O. ovata*, *O. siamensis*, and *O. lenticularis* cells have been reported (Chang et al. 2000), and detection of palytoxin-like compounds was evidenced in *O. siamensis* (Rhodes et al. 2000).

The Caribbean Sea harbors eight of the nine species of *Ostreopsis* that has been described thus far (Faust et al. 1996, Faust 1999). *Ostreopsis heptagona*, *O. lenticularis*, *O. ovata*, and *O. siamensis* appear to be the most abundant species. Our findings showed that *O. heptagona* (Figure 52) was the most frequent species in our samples, although generally the occurrence of all *Ostreopsis* species was near 10%. We did not observe *O. lenticularis*, despite its reported presence in some regions of the Caribbean Sea (Faust et al. 1996, Ashton et al. 2003). Indeed, there is not enough information to differentiate *O. lenticularis* from *O. siamensis* based on morphological features alone. Size and cell shape are the same in both species, and the main difference is the presence of two series of pores of different size in *O. lenticularis* (Fukuyo 1981). However, Faust et al. (1996) described two types of pores in *O. siamensis* and did not take this character into account in their description of *O. lenticularis*. This taxonomic ambiguity makes the strict distinction of these species impossible. Similarly, *O. belizeanus* Faust, *O. caribbeanus* Faust, and *O. marinus* Faust were not found in the present study, despite the fact that these species were described for the first time in the coral barrier off Belize (Faust 1999).

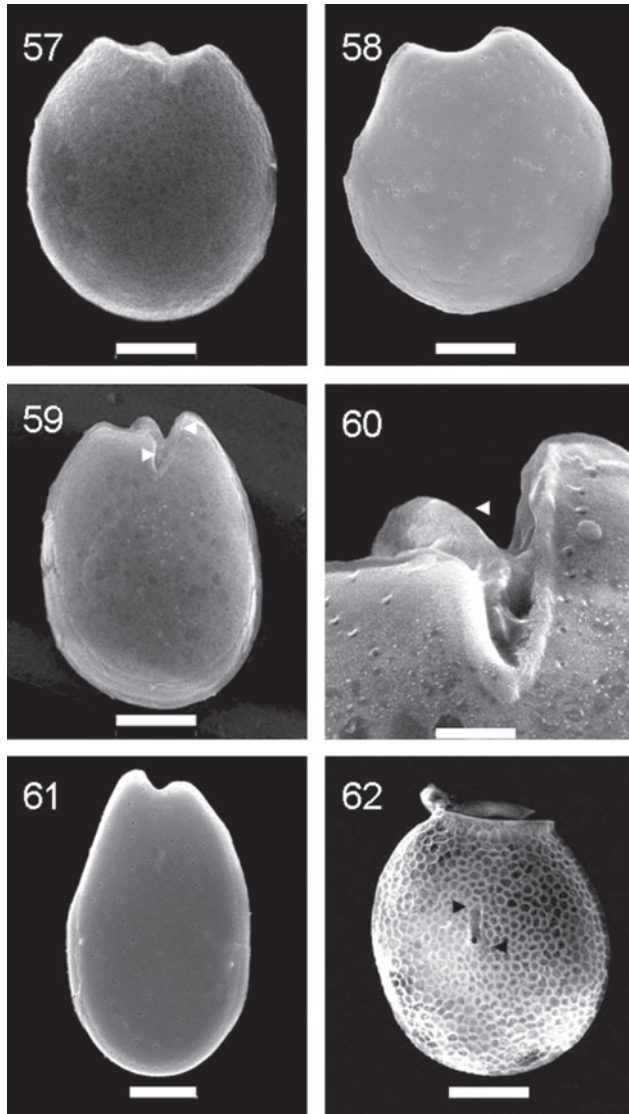
Coolia tropicalis (Figures 39–40) is a benthic species described from Belize (Faust 1995a), but it has been found also in the Indo-Pacific tropical waters (Mohammad-Noor et al. 2013, Ho and Nguyen 2014). In the Mexican Caribbean, it is a very conspicuous species where it can be found along the entire coast on a variety of macroalgae. However, further work is needed on the diversity of this genus given the increase in the number of species that has been described in the last 13 years (Ten-Hage et al. 2000, Fraga et al. 2008, Chui-Pin et al. 2010).



Figures 47–56: Scanning electron micrographs of benthic-epiphytic dinoflagellates. (47) *Amphidinium* cf. *carterae* from Tulum, ventral view. (48) *Bysmatrum caponii* from Akumal, ventral view. (49) *Sinophysis canaliculata* from Akumal, right lateral view. (50–51) *Gambierdiscus* cf. *carolinianus* from Cozumel: apical and antapical views, respectively. (52) *Ostreopsis heptagona* from Xcalak, apical view. (53–54) *Prorocentrum hoffmannianum* from Sian ka'an: left and right valves, respectively. (55–56) *Prorocentrum rathymum* from Puerto Morelos: left and right valves, respectively. Po, pore. Scale bars: 47=2 μ m; 48–56=10 μ m.

Our results suggest that epiphytic dinoflagellate assemblages composed of species of *Coolia*, *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum* are distributed on macroalgae along the coast of the Mexican Caribbean.

A major implication of this finding is that, as the macroalgae increase their coverage, the toxic dinoflagellates would also increase in abundance simply because of the increased substrate availability. An increase in



Figures 57–62: Scanning electron micrographs of *Prorocentrum* and *Sinophysis*. (57) *P. emarginatum* from Akumal, right valve. (58) *Prorocentrum* sp. from Xcalak, left valve. (59–60) *P. fukuyoi* from Puerto Morelos: (59) right valve, arrowheads show v-shaped indentation; (60) close-up of indentation, arrowhead indicates the thick flange. (61) *Prorocentrum lima* from Isla Mujeres, right valve. (62) *Sinophysis canaliculata* from Puerto Morelos, dorsal view, arrowheads indicate the caniculae. Scale bars 57, 59, 61, and 62=10 μ m; 58=5 μ m; 60=2 μ m.

macroalgal coverage is associated with a loss of coral reef cover (Hoegh-Guldberg et al. 2007). These processes are currently occurring in the central and northern areas of the state of Quintana Roo because of the development and expansion of tourist infrastructure and the rapid increase of the population (Hernández-Terrones et al. 2011). Therefore, these alterations in the coastal landscape could drive the change from coral communities to

Table 2: Sites and sampling locations along the Mexican Caribbean coast.

No.	Site	Locations	Latitude °N	Longitude °W
1	Isla Contoy	IC-1	21.46874	-86.8341
2		IC-2	21.45582	-86.78620
3		IC-3	21.43405	-86.78224
4		IC-4	21.38044	-86.77774
5		IC-5	21.38141	-86.77826
6		IC-6	21.472639	-86.78996
7	Isla Mujeres	IM-1	21.25939	-86.75732
8		IM-2	21.26544	-86.75732
9	Puerto Morelos	PM-1	20.84796	-86.87056
10		PM-2	20.87439	-86.87056
11		PM-3	20.83415	-86.87830
12	Tulum	TM-1	20.20598	-87.42623
13		TM-2	20.19924	-87.42986
14		TM-3	20.20268	-87.42750
15		TM-4	20.17144	-87.44794
16	Akumal	AK-1	20.38413	-87.32351
17		AK-2	20.38561	-87.32318
18		AK-3	20.40237	-87.30926
19		AK-4	20.40691	-87.30390
20		AK-5	20.39280	-87.31797
21	Sian ka'an	BA-1	19.8276	-87.4526
22		BA-2	19.8190	-87.4525
23		BA-3	19.7989	-87.4525
24		BA-4	19.7989	-87.4745
25		BA-5	20.00669	-87.48172
26	Majahual	MH-1	18.7180	-87.7062
27		MH-2	18.7072	-87.7089
28		MH-3	18.7057	-87.7096
29		MH-4	18.7047	-87.709800
30	Xcalak	XK-1	18.2706	-87.8349
31		XK-2	18.2742	-87.8336
32		XK-3	18.25061	-87.82999
33		XK-4	18.2578	-87.82742
34		XK-5	18.27538	-87.82816
35	Holbox	HB-1	21.61137	-87.10651
36		HB-2	21.5995	-87.11383
37		HB-3	21.59443	-87.11141
38	Cozumel	CZ-1	20.45934	-86.98586
39		CZ-2	20.45059	-87.82999
40	Chinchorro	BCh-1	18.43711	-87.41219
41		BCh-2	18.64450	-87.40860
42		BCh-3	18.74598	-87.34710

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a macroalgal-dominated community, and consequently, increase the occurrence of ciguatera in the region.

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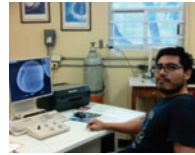
Bionotes



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Q6:
Clarify “Academic Technical Full “A””, Water Science Unit, Yucatan Center for Scientific Research” pertain to her current employer?

Graphical abstract

Antonio Almazán-Becerril, Sergio Escobar-Morales, Gabriela Rosiles-González and Francisco Valadez
Benthic-epiphytic dinoflagellates from the northern portion of the Mesoamerican Reef System

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Research article: *Prorocentrum* is the most diverse genus in the benthic-epiphytic environment in the Mexican Caribbean, with 13 species; this work also includes 15 new records of species for the region.

Keywords: benthic microalgae; Ciguatera; coral reefs; Dinophyceae; epiphytic dinoflagellates; Mexican Caribbean.

