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Marine epibenthic dinoflagellates from Malaysia - a study of live cultures and preserved samples based on light and scanning electron microscopy

N. Mohammad-Noor, N. Daugbjerg, Ø. Moestrup and A. Anton

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Marine epibenthic dinoflagellates have been collected from macroalgae, dead corals, seagrasses and sand in Malaysia and identified using light microscopy, including epifluorescence microscopy, and scanning electron microscopy. Examination of 62 samples revealed that Malaysia has rich diversity of benthic dinoflagellates, with 24 species representing 9 genera. Of these species, 8 were shown to be potentially toxic using the *Artemia* bioassay test i.e. *Prorocentrum arenarium, P. lima, P. concavum, P.* cf. *faustiae, Gambierdiscus pacificus, Ostreopsis labens, O. ovata* and *Coolia* sp. The diversity of potentially toxic species in Malaysian waters indicates that Malaysia may encounter problems with ciguatera and/or DSP. The highest species diversity was found at Sipadan Island with a total of 18 species identified. One of these is previously undescribed (*Prorocentrum sipadanensis* sp. nov.). The most common species identified at all sampling sites were *Prorocentrum lima* and *Ostreopsis ovata*. Generally, the morphology of the species identified from Malaysian waters is similar to that reported in studies elsewhere. However, new features were also observed (e.g. a pyrenoid in *Prorocentrum emarginatum* and two different-sized pores in *Ostreopsis labens*). The importance of SEM as a tool in taxonomic studies is stressed.

N. Mohammad-Noor, N. Daugbjerg and Ø. Moestrup, Section of Phycology, Department of Biology, University of Copenhagen, Øster Farimagsgade 2D, DK-1353, Copenhagen K, Denmark. E-mail: Nielsd@bi.ku.dk. – A. Anton, Biotechnology Research Institute, University Malaysia Sabah, Locked Bag 2073, 88999 Kota Kinabalu, Sabah, Malaysia.

Introduction

Marine benthic dinoflagellates are important as primary producers and play an important role in marine foodwebs (South & Whittick 1987). They live in association with macroalgae, seagrasses, corals and sand and constitute a diverse group of microalgae with a wide geographic distribution (Faust 1994). Some species have been found to cause diarrhetic shellfish poisoning (DSP) and ciguatera fish poisoning. The toxins produced are mainly okadaic acid (Murakami et al. 1982, Dickey et al. 1990, Hu et al. 1993, Barbier et al. 1999, Ten-Hage et al. 2000b), dinophysistoxin (DTX1) (Marr et al. 1992, Morton 1998, Barbier et al. 1999), maitotoxin (Holmes et al. 1991), ciguatoxin-like toxin (Holmes et al. 1991, Holmes & Lay 2002) and related derivatives.

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Malaysia has not faced any known problems related to these benthic dinoflagellate species. Studies on marine dinoflagellates were focused more on the diversity of planktonic species than on the composition of benthic species. The reason is due to the massive problems caused by planktonic dinoflagellates, which have on a number of occasions resulted in human deaths and severe economic losses to the aquaculture and fisheries industry (Puyong et al. 1998). The first and worst PSP incidence was reported in 1976 in Sabah, East Malaysia and it was caused by *Pyrodinium bahamense* Plate 1906 var. *compressum* (Böhm) Steidinger, Tester et Taylor (Roy 1977). In West Malaysia, the first PSP report was in 1993 and was caused by *Alexandrium tamiyavanichii* Balech 1994 and *A. minutum* Halim 1960 (Usup et al. 2002a, 2002b) and subsequently in 2002 by *Prorocentrum minimum* (Pavillard) Schiller (Usup et al. 2003). The State Department of Fisheries and Federal Medical and Health Service Department subsequently initiated a continuous PSP monitoring programme to safeguard public safety as well as to protect the local fisheries industry, especially in Sabah (Puyong et al. 1998).

Harmful algal blooms (HAB) have recently received more attention in Malaysia when the government launched the 3rd National Agricultural Policy (NAP3)(1992-2010). One focus of the policy is to promote and activate the marine fisheries and aquaculture industry. However, the expansion of the aquaculture industry is likely to increase events of HABs (Hallegraeff 1993) with negative effects on the marine ecosystems. Furthermore, many toxic and potentially toxic benthic dinoflagellates species have been discovered in tropical areas, including *Gambierdiscus toxicus*. This species is responsible for several thousands of human poisonings annually (Yasumoto et al. 1980) and occurs in association with a variety of substrates, including macroalgae, corals and mangrove roots (Babinchak et al. 1996). As Malaysia has a diverse marine ecosystem with several hundreds of coral reef species and numerous macroalgal and seagrass species, the existence of toxic benthic dinoflagellate communities is likely. Futhermore, the Malaysian climate is characterized by Southwest and Northwest monsoons that affect the seasonality of the macroalgae. The monsoons have also been reported to trigger the blooming of several toxic planktonic species (Usup et al. 1989, Sidabutar et al. 2000). The present study is a first attempt to fill in gaps in the knowledge of potentially toxic benthic dinoflagellates in Malaysia.

Studies on marine benthic dinoflagellates have been performed in both tropical and temperate areas (e.g. Larsen 1985, Faust 1995, 1996, Morton & Faust 1997, Turquet et al. 1998, Pearce et al. 2000, Hoppenrath 2000a, Hansen et al. 2001, Murray 2003), using live, preserved or cultured samples for species identification. Methods most often used for identification purposes are light and scanning electron microscopy. In many athecate dinoflagellates the morphology of the apical grove has recently been used at the generic level and in thecate species characters considered important are the tabulation and ornamentation of the cellulose plates, and the architecture of the periflagellar area and the intercalary bands (Faust 1994, Faust & Steidinger 1998, Quod et al. 1999). Recently, molecular techniques have also been applied to taxonomic and phylogenetic studies of dinoflagellates (e.g. Daugbjerg et al. 2000, Saldarriaga et al. 2003, Fløe-Jørgensen et al. 2004, Murray et al. 2004a). At present, 140 benthic dinoflagellate species from 28 genera have been described as marine sand dwellers (Hoppenrath et al. 2003).

The few reports on marine benthic dinoflagellates in Malaysian waters include a molecular study showing that *Ostreopsis ovata* constitutes two populations, one in the Malacca Straits and the other in the South China Sea (Leaw et al. 2001). A survey conducted in Singapore waters showed that species diversity was low, with *Ostreopsis ovata* being the dominant species (Holmes et al. 1998). A new toxin-producing species, *Gambierdiscus yasumotoi* was identified in the reef around the Singapore island of Pulau Hantu (Holmes 1998).

In this study, the species diversity of marine benthic dinoflagellates from Malaysia, mainly collected along the coast of Sabah, will be discussed. Descriptions of each species are based on light and scanning electron microscopy, and results of *Artemia* bioassay tests will be presented. The results are intended to be used for setting up a monitoring programme as well as a management programme on HAB species in Malaysia.

Materials and methods

Study areas

Malaysia is divided into two main areas, Peninsular Malaysia and East Malaysia (Sabah and Sarawak) on the island of Borneo (Fig. 1). Sandy beaches, mangrove forests and coral reefs abound in most of the islands. The coastal areas are usually dominated by macroalgae viz. *Sargassum* spp., *Padina* spp. and seagrasses. In this study, 62 samples were collected from the Peninsula and East of Malaysia (Fig. 1). In Peninsular Malaysia, samples were only collected from a single site, Port Dickson (05°44.28″N, 103° 05.00″E) (Fig. 1A). Additionally, 13 cultures were

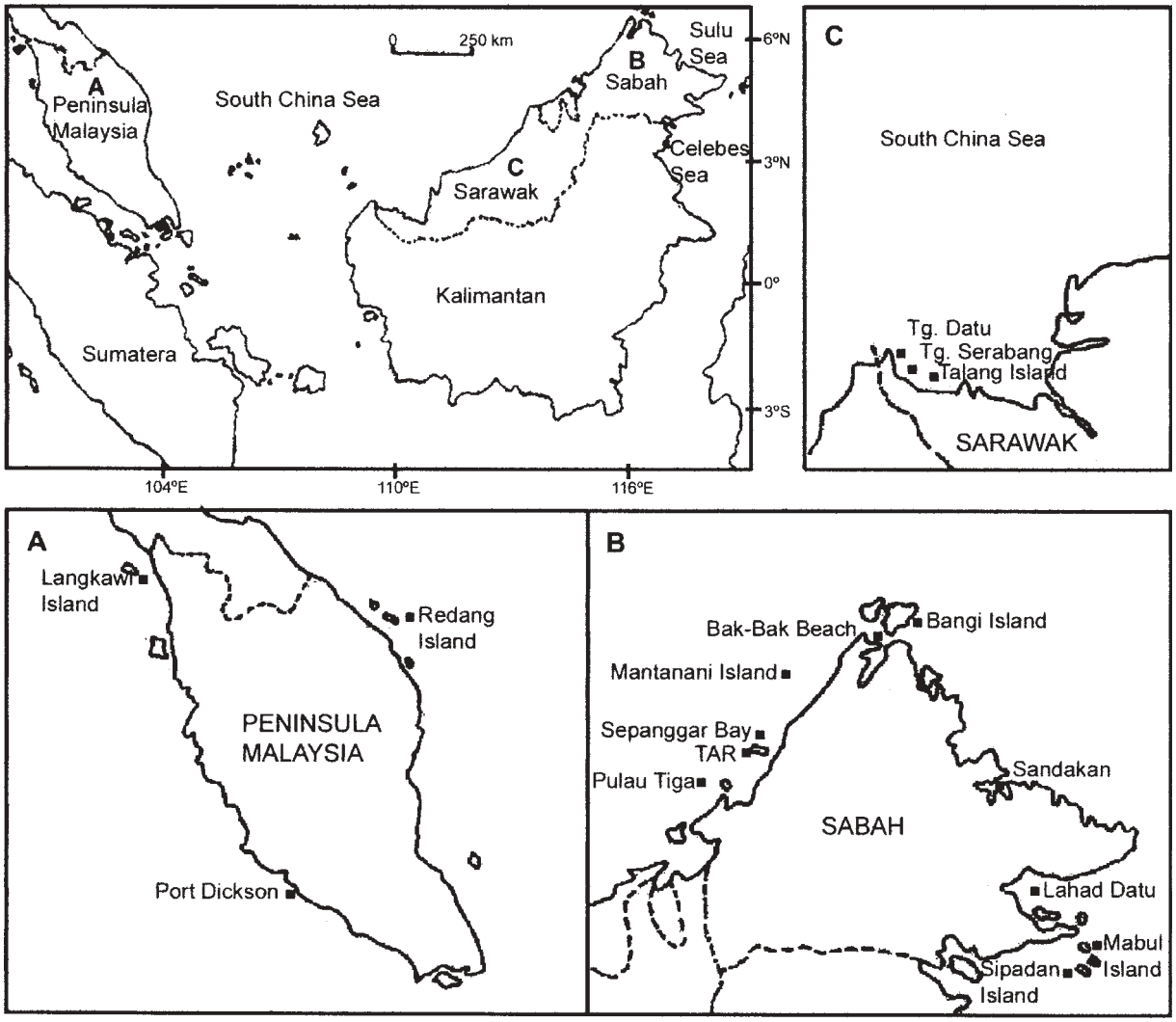

Fig. 1. Map of Malaysia showing the three sampling sites. A. Peninsula Malaysia: Langkawi Island, Port Dickson and Redang Island. B. Sabah: Pulau Tiga, TAR (Tunku Abdul Rahman Park), Sepanggar Bay, Mantanani Island, Bak-Bak Beach, Bangi Island, Sandakan, Lahad Datu, Mabul Island and Sipadan Island. C. Sarawak: Tanjung Datu, Tanjung Serabang and Talang Island.

obtained from Dr. G. Usup (National University, Malaysia) collected from Langkawi Island, Port Dickson and Redang Island (Fig. 1A). In East Malaysia, samples were collected from five sites in Sabah (Fig. 1B): Sepangar Bay, Tunku Abdul Rahman Park (06°02.42″N, 116°06.68″E), Bak-Bak Beach (07°38.65″N, 117°03.01″E), Mabul Island (04°14.84″N, 118°38.00″E) and Sipadan Island (04° 06.72″N, 118°37.75″E). Algal cultures were also established from other areas of Sabah (Pulau Tiga (05°42.71″N, 115°39.18″E), Matanani Island (06° 42.89″N, 116°20.30″E), Bangi Island, Sandakan (05° 56.73″N, 118°05.16″E) and Lahad Datu (04° 58.81″N, 118°20.86″E)). In Sarawak, samples were collected from three sites: Tanjung Datu (02° 02.23″N, 109°39.23″E), Tanjung Serabang (01° 58.94″N, 109°39.47″E) and Talang Island (01° 53.72″N, 109°46.06″E) (Fig. 1C).

Sampling methods

Macroalgae, mainly *Sargassum* spp. and *Padina* spp. and dead corals were collected at all locations. Coloured sand patches were collected at Port Dickson, Peninsula Malaysia. The macroalgae were

placed in clean plastic containers and shaken vigorously. Live and dead corals were scrubbed using a household brush, to separate live cells from the substrate. All samples were sieved through 125-μm and 20-μm mesh sieves. A portion of each sample was preserved with Lugol's iodine or 5% formalin. Live samples were brought to the laboratory, with the least possible delay at temperatures of 24 to 26ºC. In the laboratory, clonal cultures were initiated by isolating single cells using a micropipette and placing them in multi-well plates (24 wells) containing 1 ml of ES-DK medium (Kokinos & Anderson 1995). All stock cultures were maintained at 26-27ºC, 30 μmol photons $m^{-2}s^{-1}$, a 12:12 h light: dark regime and salinities of 32 psu.

Light microscopy

Micrographs were taken on an Olympus BX 60 light microscope equipped with Nomarski differential interference contrast and connected to an Olympus digital camera DP10. For visualization of thecal plates and valve pores, cells were stained with 5mg/ml of calco-fluor white (Fritz & Triemer 1985) and observed under blue light (405 nm excitation and 420 nm emission). Cell dimensions were determined using an eyepiece micrometer at 400× magnification. Morphometrics were based on measurements of 25 - 30 cultured cells. Measurements of fixed cells were based on ≤ 5 cells.

Scanning electron microscopy

Live samples were fixed for approx. 45 min with 2% OsO_4 in distilled water, rinsed in distilled water for 1 h to remove salt and fixatives, dehydrated using a graded series of ethanol (30 – 99.9%), critical-point dried and coated with a layer of platinum-palladium. For samples preserved in Lugol's iodine and 5% formalin, cells were washed with distilled water and sonicated for 30 s to 1 min before being postfixed with 2% OsO_4. The samples were then processed following the scanning procedure described above. A total of 124 stubs were observed and micrographs were taken on JEOL JSM-6335F field emission scanning electron microscope. For *Prorocentrum* spp. and *Ostreopsis* spp., numbers of valve pores and marginal pores were counted from the scanning electron micrographs in at least 10 cells of each species. The size and distance between valve pores were determined from the scanning electron micrographs at 10,000× magnification for at least 5 cells of each species as recommended by Faust (1991). However, the determination of size, number of valve pores and marginal pores of species identified from preserved samples were based on ≤ 5 cells.

Cryopreservation

This method was applied to improve preservation of species producing large quantities of mucus. *Prorocentrum lima* was chosen as a test organism. One ml of a live sample was transferred into a Swinnex 13 filterholder (Millipore) and left for at least 2 h. During this period, the sample was not allowed to dry. The sample was mounted on a stub, frozen with liquid nitrogen, and coated with a layer of platinum-palladium. The sample was then examined in the electron microscope.

Toxicity

Cultures were tested for lethality to the crustacean *Artemia franciscana* following the 'ARTOXKIT M' standard procedure (MicroBioTests Inc.). Dried eggs were incubated in darkness in 12 ml of filtered seawater for 24 h at 25°C. The hatched *A. franciscana* were separated from the eggs and incubated for another 24 h at 25°C in the dark to allow the larvae to molt to the second or third instar stage. The bioassay tests were performed in 24-well plates at 25°C in the dark by exposing in each well 10 ±2 cells of *A. franciscana* to 1 ml of culture containing 1000-2000 cells per ml. All tests were performed in 3 replicates. After 24 h, the number of dead larvae were counted. Larvae were considered dead if they did not exhibit any internal or external movements during 10 s of observation. Filtered seawater was used for control.

Results

Taxonomy

Twenty four species of dinoflagellates from the following 9 genera were identified: *Prorocentrum, Sinophysis, Gambierdiscus, Coolia, Ostreopsis*, *Amphidinium, Pileidinium, Bysmatrum* and *Peridinium*. The 8 genera represent 5 orders : Prorocentrales Lemmermann 1910, Dinophysiales Kofoid 1926, Gonyaulacales F. J. R. Taylor 1980, Gymnodiniales Apstein 1909 and Peridiniales Haeckel 1894. The taxonomic position of *Pileidinium* is uncertain and therefore the genus is placed as incertae sedis.The taxonomical scheme suggested by Fensome et al. (1993) is applied here. Below, each species is described and the morphology is compared with pre-

vious descriptions. Previous records of the species and results of bioassay tests are also presented. Prior to species descriptions, the orders to which the species belong will be briefly described.

Order Prorocentrales Lemmermann 1910

The order Prorocentrales is characterized by armoured, bivalvate cells with desmokont flagellar insertion, an anterior periflagellar area and neither cingulum nor sulcus (Steidinger & Tangen 1996). Species possess relatively simple morphological characteristics and are generally more easily identified compared to other armoured dinoflagellates. Two genera are assigned to the order, *Prorocentrum* Ehrenberg 1834 and *Mesoporos* Lillick 1937. The latter differs by having a large central cone-shaped pore in each valve. *Mesoporos* is monotypic and includes only *M. perforatus* (Gran) Lillick 1937.

The genus *Prorocentrum* has been studied extensively and approx. 70 species are currently recognized (Faust et al. 1999). In the 1990s, studies on the genus *Prorocentrum* became more numerous when many species were found to produce toxins (e. g. Marr et al. 1992, Morton 1998, Prokic et al. 1998, Barbier et al. 1999, Ten-Hage et al. 2000b). Species in high cell densities are known from the benthic environment and live in association with macroalgae or floating detritus, in sand or other sediments, attached to coral rubble, algal turf, oyster racks and mussel lines, or from the water column (e.g. Bomber et al. 1988, Faust 1990, 1991, Hansen et al. 2001, Rhodes et al. 2001). Features used for species identification are cell shape and size, the micromorphology of the valve surface, the architecture of the periflagellar area and the pattern of the intercalary band (Faust 1990, 1991). In this study we identified eleven benthic species of *Prorocentrum* and these will be described in alphabetical order.

Prorocentrum arenarium Faust 1994

Figs 2a-j, 13a,b.

Previous descriptions: Faust (1994): figs 14-21; Faust & Gulledge (2002): figs 1-6, pl. 37; Grzebyk et al. (1998): figs 1-3; Hansen et al. (2001): pl. 3, figs A-C, pl. 6, fig. A.

Taxonomic remarks: Prorocentrum arenarium is a photosynthetic species with golden-brown chloroplasts, a centrally located pyrenoid and a posterior nucleus (Fig. 2a). Cells are broadly ovate to round in valve view (Figs 2a - f, 13a). Cell size ranges from 42 to 45 μm (44 ± 1.0) in length and 35 to 40 μm (38 ± 1.2) in width (n = 30). Both valves are slightly concave in lateral view (Fig. 2g). The thecal surface is smooth, and relatively large pores are randomly distributed except in the centre (Figs 2b, d - f). The pores are kidney-shaped to oblong with smooth edges (Figs 2j, 13b). Each valve has approx. 108 - 135 pores excluding marginal pores. The pores can easily be observed under the light microscope (Faust & Gulledge 2002) (Figs 2b, d). The distance between pores is 1.4 to 5.1 μm and the pores are 0.3 - 0.7 μm in length and 0.1 - 0.4 μm in width. Both valves have distinct oblong marginal pores (Figs 2e - g). They number approx. 61 - 73 per valve. The periflagellar area is a broad V-shaped depression in the right valve (Fig. 2h), composed of *c*. 8 platelets (not shown). The flagellar pore is slightly larger than the auxiliary pore (Fig. 2h). Both the longitudinal and transverse flagellum arise from the flagellar pore (Fig. 2i). The flagellar pore and auxiliary pore are partly surrounded by a small curved apical collar (Fig. 2h). An apical spine is absent. The left valve has a flat or slightly curved anterior end (Fig. 2h). The intercalary band is smooth (Fig. 2g). In older cells, it becomes wider. In valve view, the intercalary band is seen as a rim-like structure around the cell (Figs 2e - g).

A comparison with the descriptions by Faust (1994), Grzebyk et al. (1998) and Hansen et al. (2001) showed that *Prorocentrum arenarium* collected from Sipadan Island differed somewhat in size (Table 1). It is larger than *P. arenarium* described by Faust (1994) and has a high number of valve and marginal pores. The cell size however, is similar to that described by Grzebyk et al. (1998). The curved apical collar that partly surrounds the flagellar and auxiliary pore was also reported by Grzebyk et al. (1998), but no ornamentation of the periflagellar area was described by Faust (1994) and Hansen et al. (2001).

Observations: Prorocentrum arenarium was associated with *Padina* spp., *Sargassum* spp. and seagrasses. It was found in Sipadan Island and Tunku Abdul Rahman Park, Sabah.

Previous records: *Prorocentrum arenarium* has been found previously among sand grains, attached to coral rubble (Faust 1994) and algal turf (Grzebyk et al. 1998). It has been recorded from Carrie Bow Cay, Belize (Faust 1994), the South-Western Indian Ocean (Ten-Hage et al. 2000b, Grzebyk et al. 1998) and the Western Indian Ocean (Hansen et al. 2001).

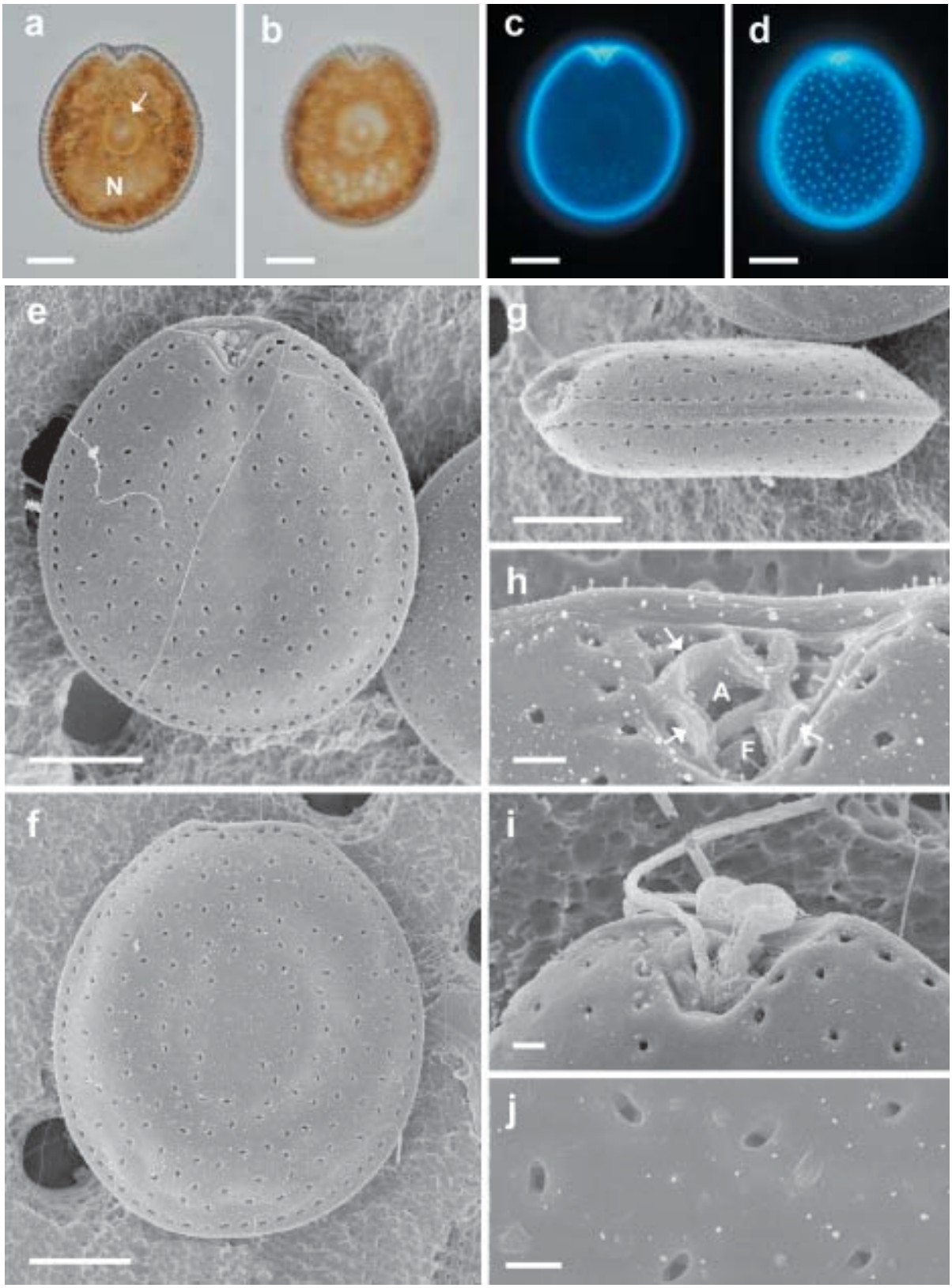
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Table 1. Comparison of cell size and morphological features in *Prorocentrum arenarium*.

Characteristics	This study	References
Cell size (μm) L=length, W=width D=diameter	L: 42-45, W: 35-40	D: 30-32 (Faust 1994) D: 36-42 (Grzebyk et al. 1998) D: 30-32 (Hansen et al. 2001)
Cell shape	Broadly ovate to round	Round to slightly oval (Faust 1994) Round (Grzebyk et al. 1998) Nearly circular (Hansen et al. 2001)
Valve pores (Vp)	Vp: 108-135 L: 0.3-0.7 μm, W: 0.1-0. 4 μm	Vp: 65-73 L: 0.62 μm, W: 0.36 μm (Faust 1994)
Marginal pores (Mp)	Mp: 61-73	Mp: 50-57 (Faust 1994)
Periflagellar area	Small curved apical collar	Small curved apical collar (Grzebyk et al. 1998) Lack of ornamentation (Faust 1994, Hansen et al. 2001)
	Approx. 8 platelets	About 8 platelets (Faust 1994)
Intercalary band	Smooth	Smooth (Faust 1994, Hansen et al. 2001)
Pyrenoid	Present	Not mentioned (Faust 1994) Present (Hansen et al. 2001) Prominent central pyrenoid (Faust & Gulledge 2002)

Toxicology: The bioassay test showed that *P. arenarium* was toxic to *Artemia franciscana*. A low density of the algae (23 cells/ml) resulted in 90% mortality of *A. franciscana*. This species has been reported to produce okadaic acid (Ten-Hage et al. 2000b).

Prorocentrum concavum Fukuyo 1981

Figs 3a-j, 14a-c.

Previous descriptions: Fukuyo (1981): figs 13-19, fig. 49; Faust (1990): figs 25-28; Faust & Gulledge (2002): pl. 40, figs 1-7; Hansen et al. (2001): pls 3F & 6D.

Taxonomic remarks: Prorocentrum concavum is photosynthetic with a golden-brown chloroplast, a central pyrenoid and the nucleus at the posterior end (Fig. 3a). Cells are round to oval in valve view (Figs 3a - f, 14a). The right valve is concave in the centre and the left valve is flattened in lateral apical view (Fig. 3g). The cell measures 43 - 53 μm (49 ± 2.5 μm) in length and 38 - 48 μm (45 ± 2.9 μm) in width (n = 30). The thecal surface is rugose with numerous scattered pores, some perhaps trichocyst pores, the pores lacking in the middle (Figs 3b, d - f). In a few cells the pores are arranged like a 'C' (not shown). The pores are located in shallow depressions and surrounded by a ring-like structure (Figs 3j, 14b, c). The pore

Figs 2a-j. *Prorocentrum arenarium*. 2a, b: Light micrographs (DIC) showing broadly ovate to round cells; 2a: cell with golden-brown chloroplast, central pyrenoid (arrow) and posterior nucleus (N); 2b: valve surface with randomly distributed valve pores; 2c, d: epifluorescence microscopy; 2c: cell outline; 2d: randomly distributed valve pores on the valve surface but lacking in the centre; 2e-j: SEM; 2e: right valve with smooth thecal surface, scattered valve pores and evenly spaced marginal pores; 2f: left valve with flat or slightly curved anterior end; 2g: lateral view, both valves are slightly concave and the intercalary band is smooth; 2h: the periflagellar area is broadly V-shaped, and consists of approx. 8 platelets; flagellar pore (F) and auxiliary pore (A) are partly surrounded by a curved apical collar (arrows); 2i: both the longitudinal and the transverse flagellum arise from the flagellar pore; 2j: kidney-shaped to oblong, smooth-edged valve pores. – Scale bars in Figs 2a-g: 10 μm, Figs 2h-j: 1μm.

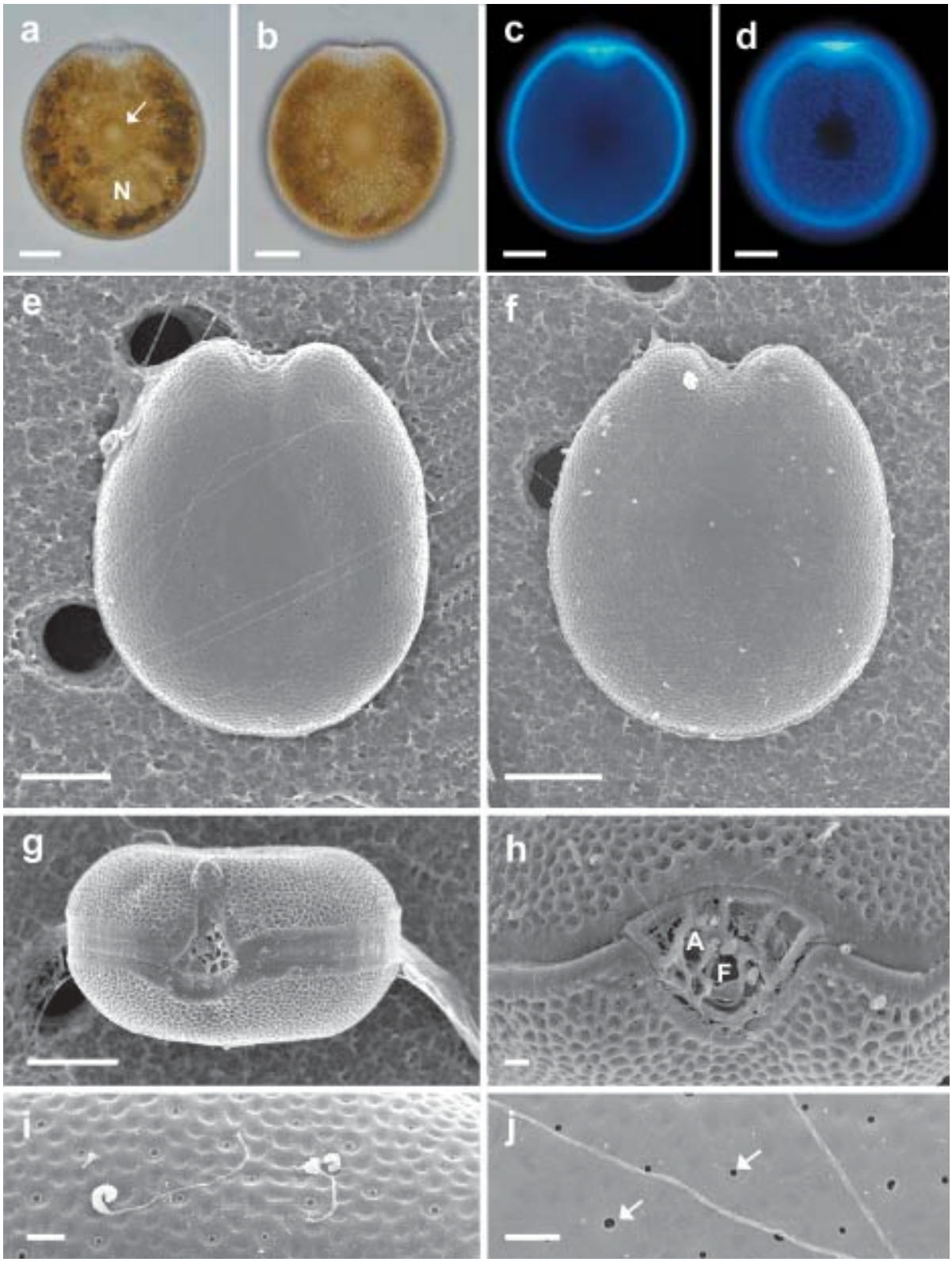
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Table 2. Comparison of cell size and morphological features in *Prorocentrum concavum*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 43-53, W: 38-48	L: 44-45, W: 40 (Fukuyo 1981) L: 50-55, W: 38-45 (Faust 1990, Faust et al. 1999)
Cell shape	Round to oval	Broadly ovate (Fukuyo 1981, Faust 1990)
Valve pores (Vp) D=diameter (μm)	Two different sizes Vp: 340-485, D: 0.12-0.23	Round opening (Faust 1990) D: 0.8 (Faust 1990)
Marginal pores	Absent	Absent (Faust 1990)
Periflagellar area	No ornamentation	No ornamentation (Fukuyo 1981, Faust 1990, Faust et al. 1999)
	Approx. 8 platelets	8 platelets (Fukuyo 1981, Faust 1990, Faust et al. 1999)
Intercalary band	Horizontally striated	Horizontally striated (Faust 1990, Faust et al. 1999)
Pyrenoid	Present	Present (Fukuyo 1981, Faust et al. 1999)

diameter is 0.12 - 0.23 μm and the distance between pores is 0.8 - 2.2 μm. Approx. 340 - 485 pores are present per valve. Ejected trichocysts possess a thickened curved head-like structure (Fig. 3i). Marginal pores are absent. The periflagellar area is triangular, rimmed and consists of approx. 8 platelets (Fig. 3h). The flagellar pore is larger than the auxiliary pore (Fig. 3h). No ornamentations are present in the periflagellar area. The left valve is concave anteriorly (Fig. 3f). The intercalary band is smooth and horizontally striated (not illustrated). The margin is narrow in newly formed cells but becomes wider in older cells.

The morphological description of *P. concavum* from Malaysia fits the descriptions of Fukuyo (1981), Faust (1990) and Faust et al. (1999). See Table 2.

Observations: Prorocentrum concavum was associated with *Padina* spp., *Sargassum* spp., seagrasses and dead corals. It was found in Tunku Abdul Rahman Park, Sepanggar Bay, Bak-Bak Beach, Mabul Island, Sipadan Island, Pulau Tiga and Tanjung Datu.

Previous records: Prorocentrum concavum was often associated with floating mangrove detritus in Hidden Lake (Faust 1990), and with algal turfs in Sainte-Marie (Madagascar), Réunion and Zanzibar Island (Hansen et al. 2001). It was first described from French Polynesia, New Caledonia and Ryukyu Island (Fukuyo 1981). It is a tropical and neritic species (Steidinger & Tangen 1996).

Toxicology: Bioassay tests showed that *P. concavum* was not toxic to *A. franciscana* even though *Artemia* larvae became immobile immediately after being mixed with *P. concavum*. The *Artemia* stopped swim-

Figs 3a-j. *Prorocentrum concavum*. 3a,b: Light micrographs (DIC) showing round to oval cells; 3a: cell with golden-brown chloroplast, centrally located pyrenoid (arrow) and a posterior nucleus (N); 3b: numerous pores are present on the thecal surface; 3c, d: epifluorescence microscopy; 3c: cell outline; 3d: numerous pores are scattered on the valve surface except in the valve middle; 3e-j: SEM; 3e: right valve showing rugose thecal surface with pores located in shallow depressions; 3f: left valve with concave anterior end; 3g: lateral apical view, the right valve is concave in the centre and the left valve is flattened; 3h: the periflagellar area is triangular, rimmed and consists of approx. 8 platelets. The flagellar pore (F) is slightly larger than the auxiliary pore (A); 3i: Ejected trichocysts are shaped as long threads with a thickened, curved, head-like structure; 3j: two different sizes of valve pores are present on the valve surface (arrows), each surrounded by a ring-like structure. – Scale bars in Figs 3a-g: 10 μm, Figs 3h-j: 1μm.

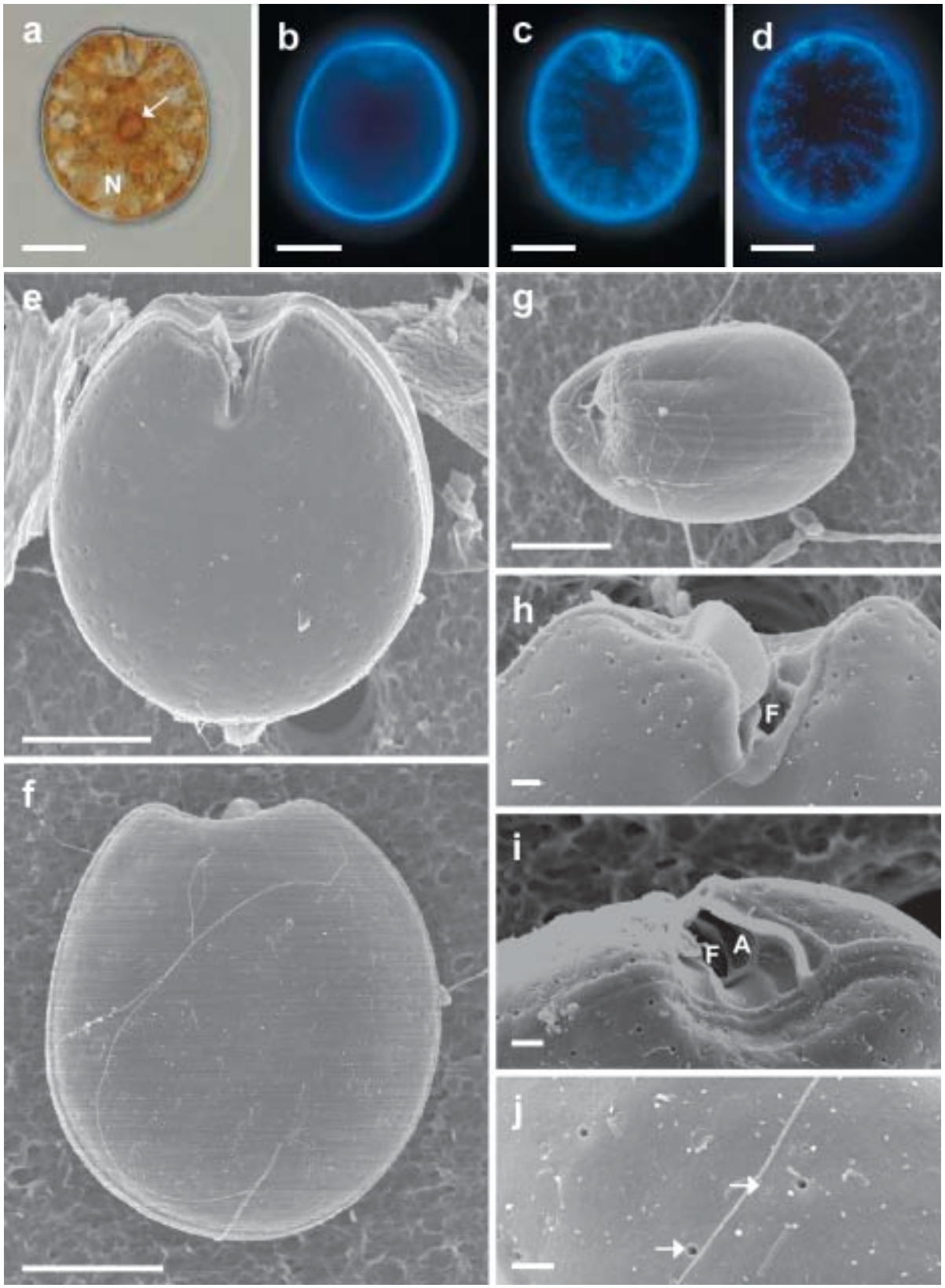
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Table 3. Comparison of cell size and morphological features in *Prorocentrum emarginatum*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 29-40, W: 28-33 L: 35-40 (Faust 1990)	L: 35-36, W: 32 (Fukuyo 1981) L: 30-40, W: 30-35 (Hansen et al. 2001)
Cell shape	Broadly ovate	Broadly ovate (Fukuyo 1981, Faust et al. 1999) Broadly ovate to rotundate (Faust 1990)
Valve pores (Vp) D=diameter (μm)	Two different sizes Vp: 100-165, D: 0.13-0.22	Two different sizes (Faust 1990) Large pores: 200, D: 0.2 (Faust 1990, Faust et al. 1999) Small pores: D: 0.1 (Faust et al. 1999)
Marginal pores	Present	Present (Faust et al. 1999)
Periflagellar area	Wing-like structure c. 5-6 platelets	One small stout spine (Fukuyo 1981) Inclined, rectangular flagellar structure (Faust 1990) Not mentioned (Fukuyo 1981, Faust 1990, Faust et al. 1999)
Intercalary band	Smooth, striated	Broad, transversely striated (Faust 1990)
Pyrenoid	Present	Absent (Hansen et al. 2001) Not mentioned (Fukuyo 1981, Faust 1990, Faust et al. 1999)

ming but were still able to move their appendages. *Prorocentrum concavum* has been reported to produce three diol esters of okadaic acid (Hu et al. 1993) and ichthyotoxin (Yasumoto et al. 1987).

Prorocentrum emarginatum Fukuyo 1981

Figs 4a-j, 15a, b.

Previous descriptions: Fukuyo (1981): figs 8-12; Faust et al. (1999): figs 3a-f.

Taxonomic remarks: Prorocentrum emarginatum is a photosynthetic species with golden-brown chloroplast, a central pyrenoid and a posterior nucleus (Fig. 4a). Cells are oval (Figs 4a- f, 15a). The right valve is convex with a slight depression in the anterior part and the left valve is convex in lateral view (Fig. 4g). The cell measures 29 - 40 μm (35 ± 2.1 μm) in length and 28 - 33 μm (31 ± 2.1 μm) in width (n = 30). The valve surface is smooth and perforated with two different sizes of pores (Figs 4e, f, j, 15b). The valve centre is devoid of pores (Figs 4c - f). The round pores are encircled by a smooth ring-like structure (Fig. 4j) and arranged radially from the periphery to the centre of the cell (Figs 4c -f). There are approx. 100 - 165 pores per valve, the pore diameter ranging from 0.13 to 0.22 μm. The distance between pores is 0.5 - 3.6 μm. Marginal pores are present. The periflagellar area is V-

Figs 4a-j. *Prorocentrum emarginatum*. 4a: Light micrograph (DIC) showing broadly oval cell shape, golden-brown chloroplast, a central pyrenoid (arrow) and a posterior nucleus (N); 4b, c, d: epifluorescence microscopy showing cell outline (4b), radially arranged valve pores from the periphery to the centre of the cell in both the right valve (4c) and the left valve (4d); 4e-j: SEM; 4e: right valve with smooth thecal surface, radially arranged valve pores from the cell margin to the centre but lacking in the middle; 4f: left valve with curved anterior end; 4g: lateral view, the right valve is convex with a slight depression anteriorly; the left valve is convex and the intercalary band is smooth and striated; 4h: the periflagellar area with flagellar pore (F) is V-shaped, rimmed, and is ornamented with a wing-like structure; 4i: the auxiliary pore (A) is obscured by the wing-like structure and almost equal in size to the flagellar pore (F); 4j: both sizes of pores are encircled by smooth ring-like structure (arrows). – Scale bars in Figs 4a-g: 10 μm, Figs 4h-j: 1μm.

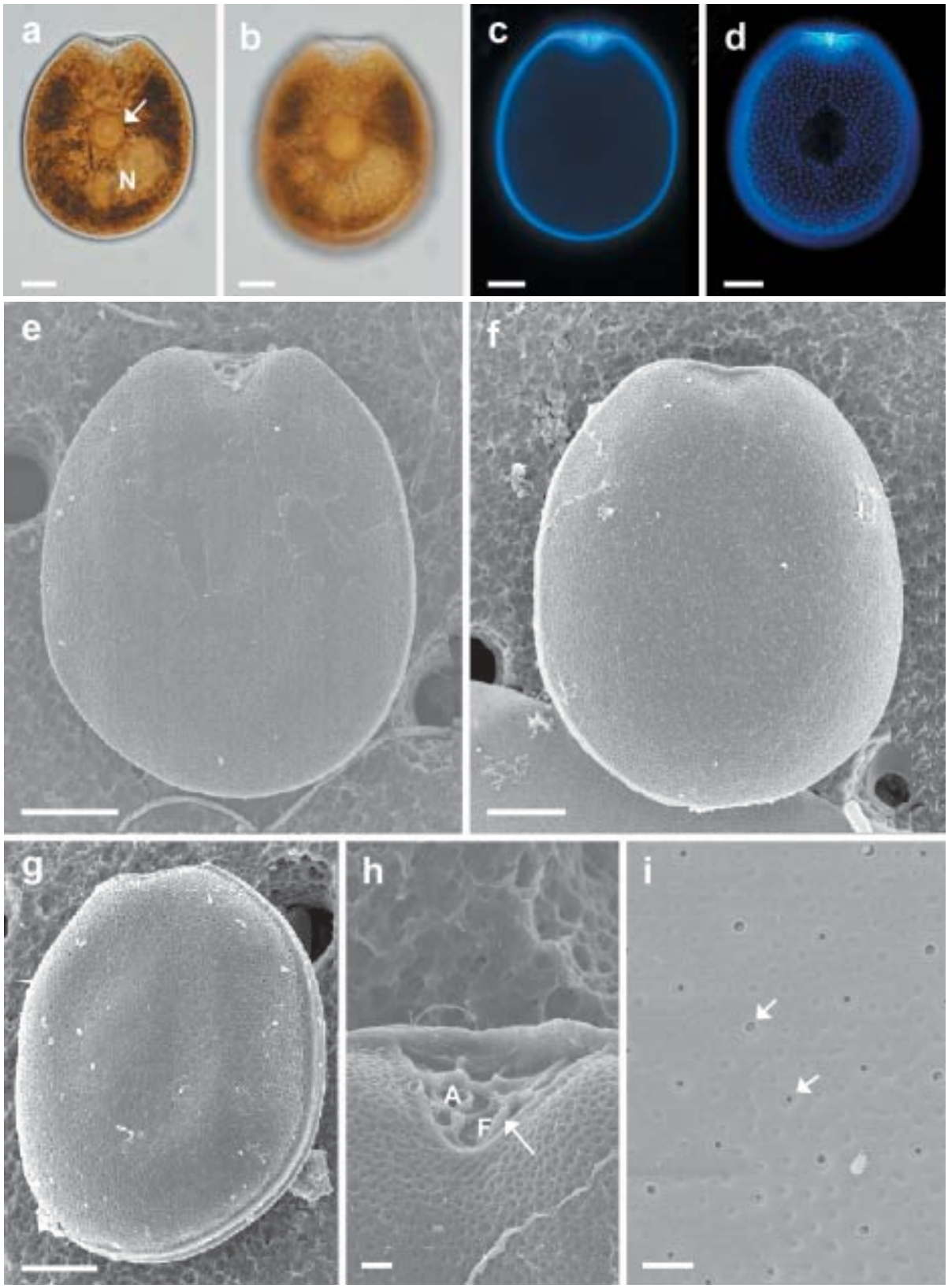
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Table 4. Comparison of cell size and morphological features in *Prorocentrum* cf. *faustiae*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 45-60, W: 38-53	L: 43-49, W: 38-42 (Morton 1998)
Cell shape	Elongate to round with round posterior end and slightly concave anterior end	Broadly ovate to rotundate (Morton 1998)
Valve pores (Vp) D=diameter (μm)	Vp: 308-477, D: 0.10-0.20	D: 0.10 (Morton 1998)
Marginal pores	Present	Present (Morton 1998)
Periflagellar area	Curved apical collar Around 8-9 platelets	No ornamentation (Morton 1998) 16 platelets (Morton 1998)
Intercalary band	Horizontally striated	Horizontally striated (Morton 1998)
Pyrenoid	Present	Present (Morton 1998)

shaped, rimmed, consists of approx. 5 to 6 platelets and is ornamented with a wing-like structure (Figs 4e, h, i). The auxiliary pore usually is obscured by this structure (Fig. 4i). The flagellar and auxiliary pores are almost equal in size (Fig. 4i). The anterior end of the left valve is concave (Fig. 4f). The intercalary band is smooth and striated (Fig. 4g).

A comparison with previous descriptions showed that *P. emarginatum* ranges widely in cell length. Previous authors have reported a central pyrenoid to be absent or it is not mentioned (Table 3).

Observations: Prorocentrum emarginatum was associated with *Sargassum* spp., *Padina* spp., seagrasses and dead corals. It was found in Tunku Abdul Rahman Park, Sepanggar Bay, Bak-Bak Beach and Sipadan Island, Sabah.

Previous records: Prorocentrum emarginatum occurred in algal samples collected on coral reefs at Ryukyu Island (Fukuyo 1981), in floating detritus from mangrove at Twin Cays, Belize (Faust 1990), in algal turf in Réunion and Zanzibar Island (Hansen et al. 2001) and in the water column in Indonesia (Sidabutar et al. 2000).

Toxicology: Prorocentrum emarginatum was not toxic to *A. franciscana*.

Prorocentrum cf. faustiae Morton 1998

Figs 5a-i, 16a, b.

Previous descriptions: Morton (1998): figs 1-4; Faust & Gulledge (2002): pl. 41, figs 1-4.

Taxonomic remarks: Prorocentrum cf. *faustiae* is a photosynthetic species with golden-brown chloroplast, a central pyrenoid and a posterior nucleus

Fig.s 5a-i. *Prorocentrum* cf. *faustiae*. 5a, b: Light micrographs (DIC) showing elongate cells with golden-brown chloroplast, a central pyrenoid (arrow) and a posterior nucleus (N); 5c, d: epifluorescence microscopy; 5c: cell outline; 5d: valve surface with numerous scattered pores except centrally; 5e-i: SEM; 5e: the right valve is rugose and perforated by valve pores; 5f: the left valve with a slightly curved anterior end; 5g: oblique valve view; left valves is almost flat; 5h: the periflagellar area is widely V-shaped, and consists of 8-9 platelets; the flagellar pore (F) is slightly larger than the auxiliary pore (A) and on the left side lined by a curved apical collar (arrow); 5i: the valve pores are uneven in size (arrows) and each pore is encircled by a smooth ring-like structure. – Scale bars in Figs 5a-g: 10 μm, Figs 5h-i: 1μm.

Table 5. Comparison of cell size and morphological features in *Prorocentrum foraminosum*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 32-34, W: 29-31	L: 46-66, W: 31-42 (Faust 1993b, Faust et al. 1999)
Cell shape	Round to oval	Oval to oblong (Faust 1993b) Oblong to ovate (Faust et al. 1999)
Valve pores (Vp) D=diameter (μm)	Vp: 300-331, D: 0.10-0.20	Vp: 270-350, D: 0.4 (Faust 1993b) Vp: c. 300 (Faust et al. 1999)
Marginal pores	Absent	Absent (Faust 1993b, Faust et al. 1999)
Periflagellar area	No ornamentation Approx. 8 platelets	No ornamentation (Faust 1993b, Faust et al. 1999) 8 platelets (Faust 1993b, Faust et al. 1999)
Intercalary band	Smooth	Smooth (Faust 1993b, Faust et al. 1999)
Pyrenoid	No data	Present (Faust 1993b)

(Fig. 5a). The cell is elongate to round with a round posterior end and a slightly concave anterior end (Figs 5a - f, 16a). Both valves are flat in lateral view (Fig. 5g). The cell measures 45 - 60 μm (52 ± 3.3 μm) in length and 38 - 53 μm (44 ± 3.0 μm) in width (n = 25 cells). The thecal surface is rugose and perforated with numerous small, round pores except in the valve centre (Figs 5b, d, g). Each pore is situated in a shallow depression of the valve surface and encircled by a smooth ring-like structure (Figs 5i, 16b, c). The distance between pores is 0.5 - 1.8 μm and the pore size is 0.1 - 0.2 μm. Approx. 308 - 477 pores are present per valve. Marginal pores are present (Fig. 5g). The periflagellar area is widely V-shaped, located on the right valve and consists of *c*. 8 to 9 platelets (Fig. 5h). The flagellar pore is larger than the auxiliary pore (Fig. 5h). The flagellar pore is lined on the left side by a curved apical collar (Fig. 5h). The anterior end of the left valve is slightly curved (Figs 5f, h) and extends slightly to surround the periflagellar area (Fig. 5h). The intercalary band is horizontally striated (not illustrated).

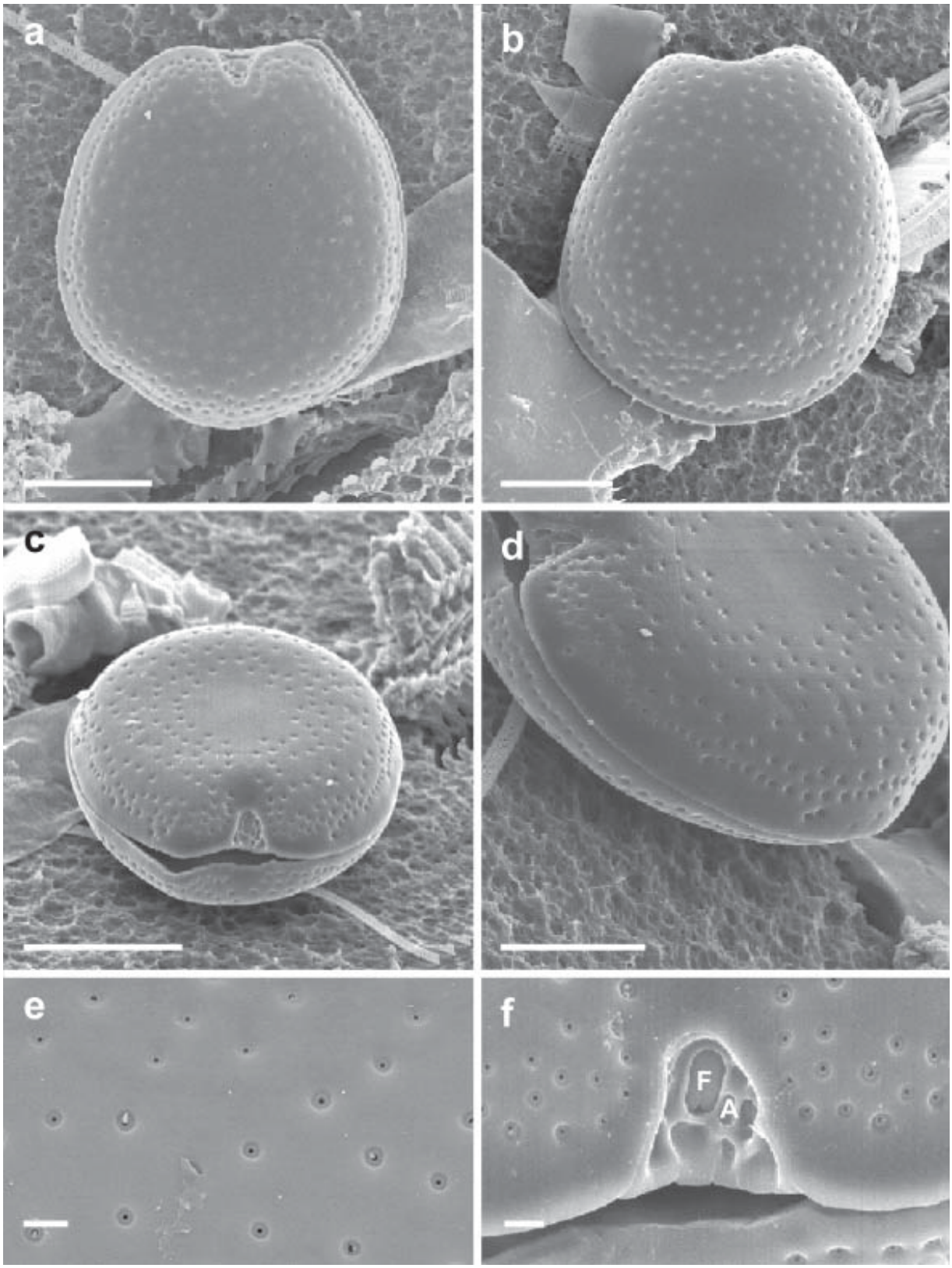
Compared with the description of Morton (1998), *P.* cf. *faustiae* from Malaysia is larger. It also has a small curved apical collar and fewer platelets in the periflagellar area (Table 4). See further in the discussion.

Observations: This species was associated with *Sargassum* spp. on Mantanani Island and Tunku Abdul Rahman Park, western Sabah.

Previous record: Prorocentrum faustiae was found on macrophytes in the reef flats of Heron Island, Australian Barrier Reef (Morton 1998).

Toxicology: A bioassay test did not indicate toxicity to *A. franciscana*. However, the larvae became immobile immediately after being mixed with *P.* cf. *faustiae*. After 24h, the *Artemia* were still able to move their appendages. *Prorocentrum* cf. *faustiae* has been reported to produce okadaic acid (OA) and dinophysistoxin-1 (DTX1) (Morton 1998).

Figs 6a-f. *Prorocentrum foraminosum*. 6a-f : SEM; 6a: the right valve showing the round to oval cell. The thecal surface is smooth with scattered valve pores except in the middle; 6b: the left valve is slightly concave at the anterior end; 6c: lateral apical view showing numerous pores except in the centre; 6d: lateral view, marginal pores are absent and the intercalary band is smooth; 6e: valve pores are located in shallow depressions and lined by ring-like structures; 6f: the periflagellar area is small and triangular and consists of approx. 8 platelets. The flagellar pore (F) is larger than the auxiliary pore (A). – Scale bars in Figs 6a-d: 10 μm, Figs 6e-f: 1 μm.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Prorocentrum foraminosum Faust 1993

Figs 6a-f, 17a, b.

Previous descriptions: Faust (1993b): figs 7-13; Faust et al. (1999): figs 4a-g.

Taxonomic remarks: Cells are round to oval in valve view (Figs 6a, b, 17a). The cell size ranges from 32 to 34 μm (33 ± 1.4 μm) in length and 29 to 31μm (30 ± 1.4 μm) in width (n = 2 cells). The thecal surface is smooth with numerous scattered pores, except in the middle (Figs 6a - d). The pores are located in shallow depressions and each pore is bordered by a ring-like structure (Figs 6e, 17b). The pore diameter is 0.10 - 0.20 μm. Approx. 300 - 331 pores are present per valve. Marginal pores are absent (Figs 6a - d). The periflagellar area is small, triangular and situated on the right valve. It consists of approx. 8 platelets (Fig. 6f). The flagellar pore is larger than the auxiliary pore (Fig. 6f). No ornamentations are present in the periflagellar area (Fig. 6f). The left valve is slightly concave anteriorly (Figs 6a, b). The intercalary band is smooth (Figs 6c, d).

According to Faust 1993b, *P. foraminosum* is a photosynthetic species, with a central pyrenoid and the nucleus in the posterior end. The morphological description of *P. foraminosum* from Malaysia fits with the original description by Faust (1993b). Only, the cell shape is more round to oval and the size is smaller (Table 5).

Observations: This species was only observed in preserved samples collected from *Sargassum* spp. and dead coral in Tunku Abdul Rahman Park and Bak-Bak Beach.

Previous record: Prorocentrum foraminosum was identified from floating detritus in Twin Cays (Faust 1993b). It may be misidentified under the light microscope as *P. lima* due to the similar pore arrangements on the thecal surfaces. However, *P. lima* has prominent marginal pores while *P. foraminosum* lacks these.

Toxicology: Unknown

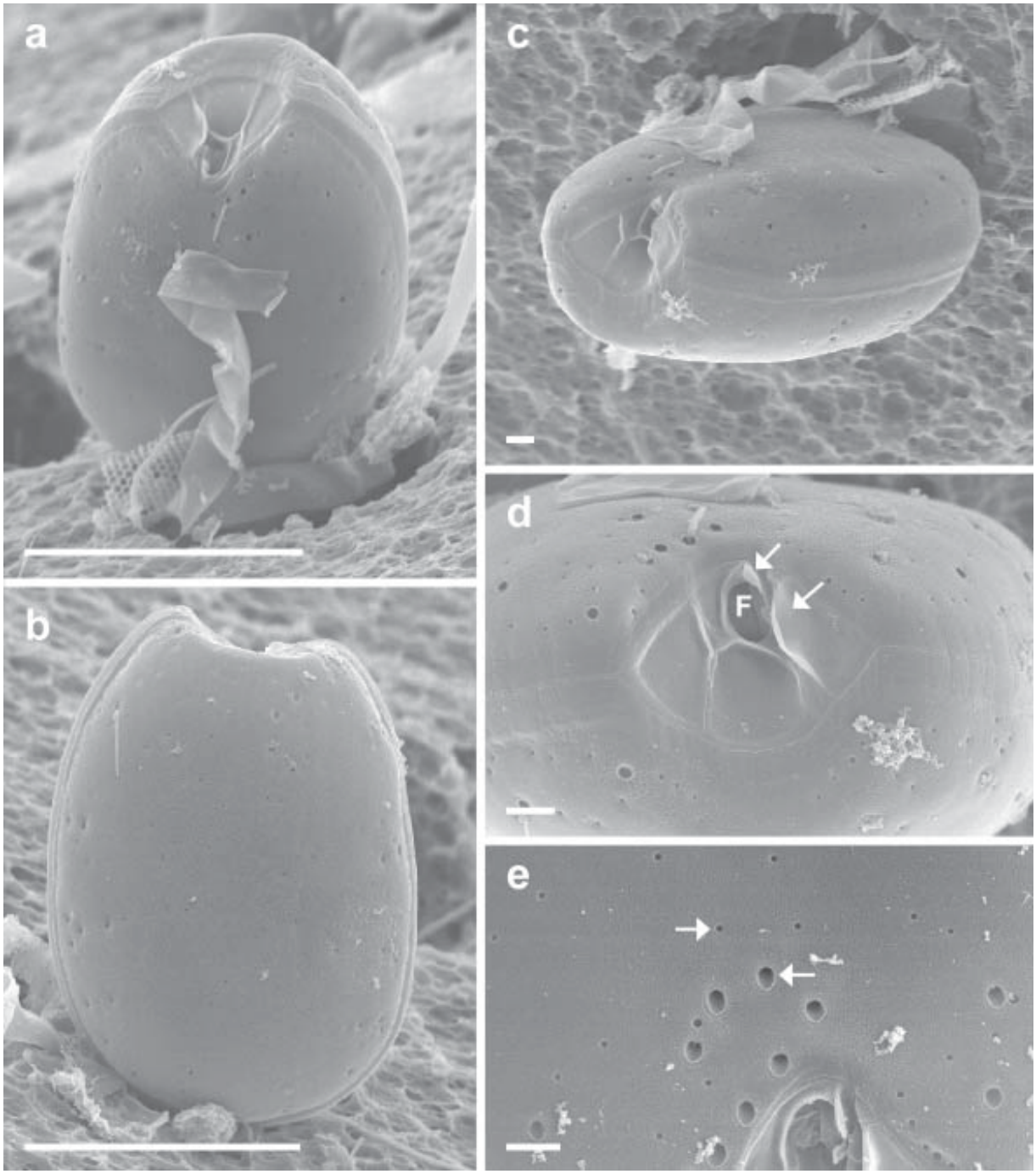
Prorocentrum formosum Faust 1993

Figs 7a-e, 18a, b.

Previous description: Faust (1993b): figs 14-22.

Table 6. Comparison of cell size and morphological features in *Prorocentrum formosum*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 18-21, W: 13-15	L: 25-28, W: 15-16 (Faust 1993b)
Cell shape	Oval to oblong	Ovate (Faust 1993b)
Valve pores (Vp) D=diameter (μm) Small pores (Sp) Large pores (Lp) Trichocyst pores (Tp)	Two different sizes Sp: 75-119, D: 0.09-0.24 Lp: 24-39, D: 0.29-0.38	Two different sizes (Faust 1993b) Vp: 42-55, D: < 0.1 Tp: D: 0.2
Marginal pores	Absent	Absent (Faust 1993b)
Periflagellar area	Two prominent wings 5-6 platelets	Two curved apical plate and shallow flange surrounds the flagellar pore (Faust 1993b) 5-6 platelets (Faust 1993b)
Intercalary band	Transversely striated	Transversely striated (Faust 1993b)
Pyrenoid	No data	Absent (Faust 1993b)



Figs 7a-e. *Prorocentrum formosum*. 7a-e: SEM; 7a: the right valve showing smooth thecal surface perforated by two different sizes of pores; 7b: the left valve showing oval to oblong cell with larger pores arranged in a characteristic pattern and smaller pores scattered on the valve surface; 7c: lateral view, the right valve is slightly concave near the periflagellar area, and the left valve is convex; 7d: periflagellar area is widely triangular, consists of 5-6 platelets and is ornamented with two prominent lists of different sizes (arrows). The flagellar pore (F) is partly surrounded by the smaller list; 7e: the two different sizes of pores (arrows). – Scale bars in Figs 7a-b: 10 μm, Figs 7c-e: 1μm.

Taxonomic remarks: Cells are oval to oblong in valve view (Figs 7a, b, 18a). The right valve is slightly concave near the periflagellar area and the left valve is convex in lateral view (Fig. 7c). The cell measures 18 - 21 μm (19 ± 1.3 μm) in length and 13 - 15 μm (14 ± 0.7 μm) in width (n = 5 cells). The thecal surface is smooth and perforated by two different sizes of valve pores (Figs 7a - e, 18b). The small pores are circular, have smooth edges, are uneven in size and occur scattered on the valve surface, except in the middle (Figs 7a, b). The pore diameter is 0.09 - 0.24 μm and approx. 75 - 119 pores are present on each valve. The larger pores are oblong to round, with smooth edges, and arranged in a distinct pattern (Figs 7a, b). The pore diameter ranges from 0.29 to 0.38 μm, and approx. 24 to 39 pores are present on each valve. The periflagellar area is widely triangular, ornamented with two prominent lists of different size, and consists of 5 to 6 platelets (Fig. 7d). Both lists are situated on one sides of the periflagellar area, one larger than the other (Fig. 7d). The larger list was described as a curved apical plate by Faust (1993b). The flagellar pore is partly surrounded by a flange (Fig. 7d). No auxiliary pore was observed (Fig. 7d). The left valve is concave at the anterior end (Fig. 7b). The intercalary band is transversely striated (Figs 7c, d).

According to Faust (1993b), *P. formosum* is a photosynthetic species containing cinnamon-brown chloroplast; a pyrenoid is lacking and the nucleus is situated in the anterior part of the cell.

The morphological features of *P. formosum* from Malaysia generally fits with the original description by Faust (1993b). However, *P. formosum* from Malaysia is smaller and has more valve pores (Table 6).

Observations: This species was rarely observed in preserved samples collected from Sipadan Island, Mabul Island and Tunku Abdul Rahman Park. It was associated with *Sargassum* spp., *Padina* spp. and seagrasses.

Previous record: Prorocentrum formosum was identified from surface sediment and floating detritus in Twin Cays, Belize (Faust 1993b). It may form blooms which colour the water golden brown.

Toxicology: Unknown

Prorocentrum lima (Ehrenberg) Dodge 1975

Figs 8a-j, 19a, b.

Synonyms : Cryptomonas lima Ehrenberg 1860.
Exuviella marina Cienkowski 1881.
Exuviella lima (Ehrenberg) Bütschli 1885.
Exuviella marina var. *lima* (Ehrenberg) Schiller 1933.

Previous descriptions: Faust (1991): figs 3-9; Faust et al. (1999): figs 6a-h; Faust & Gulledge (2002): figs 1-7, pl. 43; Maranda et al. (1999): figs 2a-c; Hansen et al. (2001): pl. 5A-D, pl. 6G.

Taxonomic remarks: Prorocentrum lima is photosynthethic with golden-brown chloroplasts, a prominent central pyrenoid and a posterior nucleus (Figs 8a, b). Cells are ovate to oblong in valve view, widest in the middle (Figs 8a - f, 19a) or more rarely of equal width from the anterior to the posterior end (Fig. 8g). The cell is 38 - 45 μm long and 27 - 38 μm wide, with small differences between collection sites (Table 7). The cell margin is round at the posterior end and flat at the anterior end (Figs 8a - f). The left valve is concave in oblique valve view (Fig. 8h). The thecal surface is smooth with scattered pores (Figs 8b, d - g). The pores are oblong to kidney-shaped (Fig. 19b), sometimes round, and have smooth edges (Fig. 8j). The distance between pores is 1.3 - 4.2 μm and the pore length 0.2 - 0.4 μm. Approx. 61 - 91 pores per valve are present on each valve. The valve centre lacks pores (Figs 8b, d - h). Both valves have about 61 - 76 uniformly-sized marginal pores. The oblong marginal pores are evenly spaced around the periphery of the cell (Figs 8e - h).

The periflagellar area is small with a triangular depression and composed of approx. 8 platelets (Fig. 8i). An apical spine is lacking (Fig. 8i). The left valve is straight to slightly curved anteriorly (Figs 8e - g). The flagellar pore is larger than the auxiliary pore (Fig. 8i). A small curved apical collar surrounds the flagellar and the auxiliary pores (Fig. 8i). The inter-

Figs 8a-j. *Prorocentrum lima*. 8a, b: Light micrographs (DIC) showing ovate to oblong cells with maximum width in the middle; 8a: cell with golden-brown chloroplast, a central pyrenoid (arrow) and a posterior nucleus (N); 8b: cell with central pyrenoid surrounded by starch sheath; 8c, d: epifluorescence microscopy; 8c: cell outline; 8d: valve pores scattered on the valve surface; 8e-j: SEM; 8e, f: right and left valve, respectively, cryopreserved; 8e: right valve showing smooth thecal surface with valve pores except in the centre and evenly-spaced marginal pores; 8f: left valve with straight to slightly curved anterior end; 8g: cell with parallel sides; 8h: the left valve is concave; 8i: the periflagellar area is small, triangular, composed of 8 platelets and with small curved apical collars around the flagellar pore (F) and the auxiliary pore (A) (arrow). 8j: oblong to kidney-shaped valve pores. – Scale bars in Figs 8a-h: 10 μm, Figs 8i-j: 1μm.

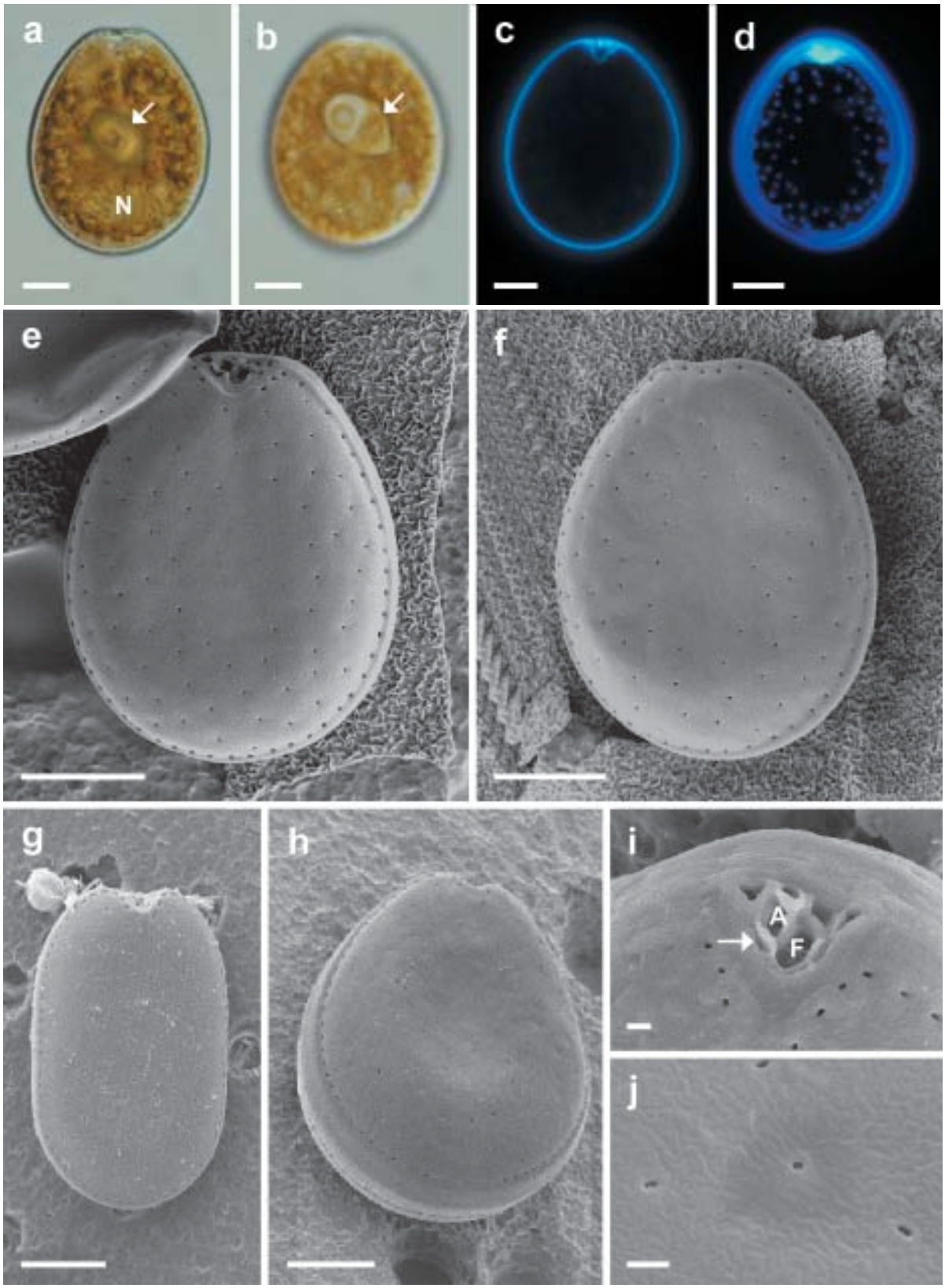

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Table 7. Comparison of cell size and morphological features in *Prorocentrum lima*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 39-43 (38 ± 2.0, n=25) W: 27-38 (32 ± 2.5, n=25) -Sipadan Island	L: 31-47, W: 22-40 (Faust 1991, Faust et al. 1999)
	L: 40-45 (42 ± 1.7, n=30) W: 33-38 (34 ± 1.2, n=30) -Pulau Tiga	L: 35-50, W: 25-45 (Hansen et al. 2001)
	L: 38-40 (38 ± 0.9, n=30) W: 28-30 (29 ± 0.9, n=30) -Mabul Island	
Cell shape	Oval to oblong	Ovate (Faust et al. 1999) Oblong to ovate (Faust 1991) Oval to oblong (Hansen et al. 2001)
Valve pores (Vp) D=diameter (μm)	Vp: 61-91, D: 0.20-0.40	Vp: c. 100 (Faust et al. 1999), 58-85, D: 0.31-0.70 (Faust 1991)
Marginal pores (Mp)	Mp: 61-76	Mp: 55-75 (Faust 1991)
Periflagellar area	Small curved apical collar	Protuberant apical collar (Faust 1991) Curved apical collar (Faust et al. 1999)
	Approx. 8 platelets	8 platelets (Faust 1991)
Intercalary band	Horizontally striated	Smooth with flared ridge (Faust 1991)
Pyrenoid	Present	Present (Faust 1991, Faust et al. 1999, Hansen et al. 2001)

calary band is horizontally striated (not illustrated). The margin is narrow in newly-formed cells but becomes wider in older cells. The morphology of *P. lima* is similar to that described elsewhere (e.g. Faust 1991, Faust et al. 1999, Faust & Gulledge 2002) (Table 7).

Observations: This species was common in all study areas, associated with seagrasses, *Sargassum* spp., *Padina* spp. or in sand. *Prorocentrum lima* was observed in Tunku Abdul Rahman Park, Sepanggar Bay, Pulau Tiga, Bak - Bak Beach, Sipadan Island, Mabul Island, Tanjung Datu, Tanjung Serabang and Port Dickson.

Previous records: Prorocentrum lima has been found to be attached to macroalgae (Faust et al. 1999), oyster racks, mussel lines (Rhodes et al. 2001), floating detritus (Faust 1990, 1991), in sediments (Faust 1990) or in the water column (Marr et al. 1992, Maranda et al. 1999, Sidabutar et al. 2000). It is widely distributed in both temperate and tropical regions (Faust 1991), including South-East Asia (e.g. Indonesian (Sidabutar et al. 2000) and Singaporean reefs (Holmes et al. 1998).

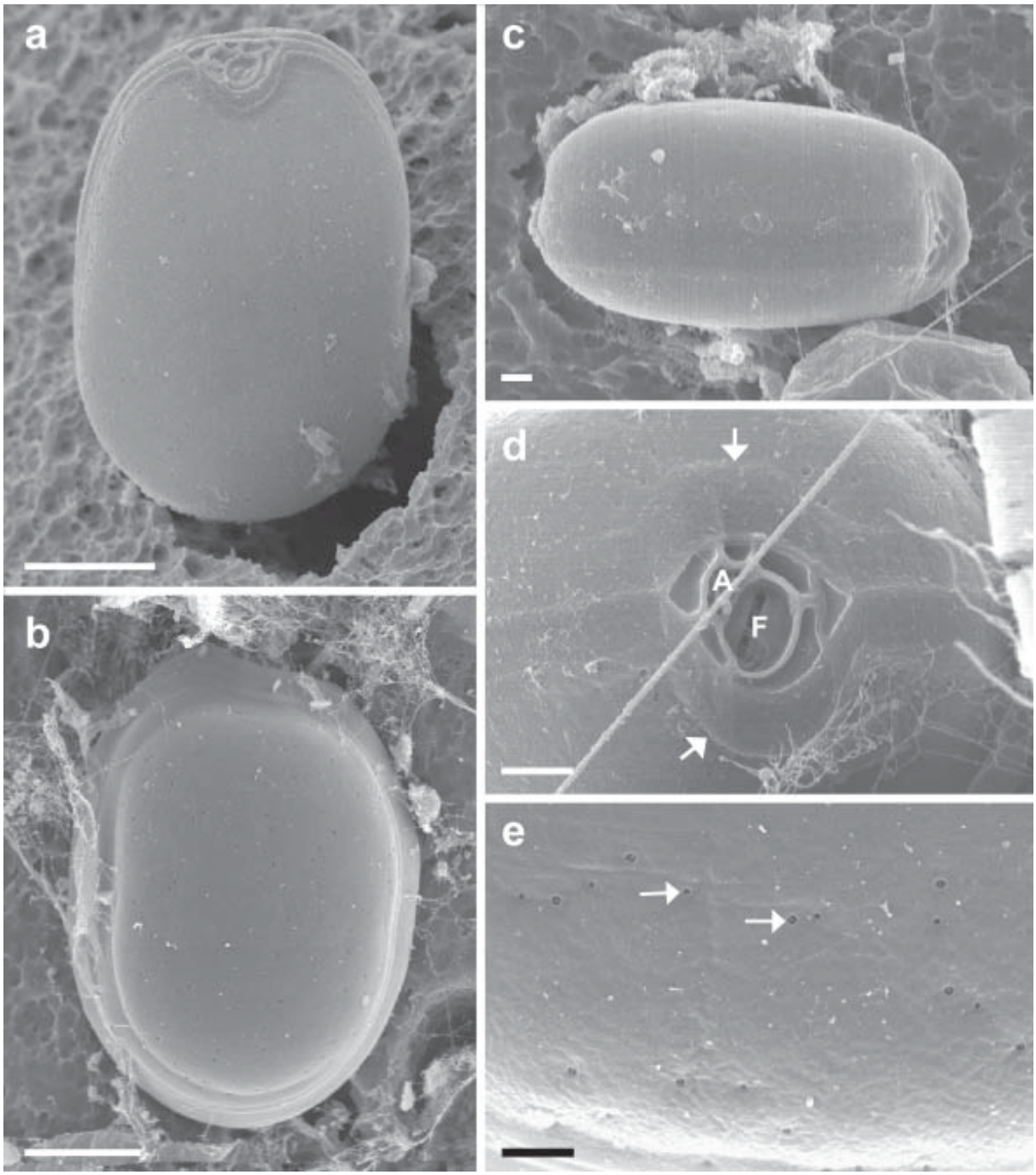
Toxicology: The toxicity of 3 strains from 3 different sites was tested using the *Artemia* bioassay. All strains showed high toxicity to *Artemia* larvae. *Prorocentrum lima* is a known DSP producer (Prokic et al. 1998, Sechet et al. 1998) and produces okadaic acid (OA) and dinophysistoxin (DTX1) (Marr et al. 1992, Barbier et al. 1999).

Prorocentrum norrisianum Faust 1997

Figs 9a-e, 20a, b.

Previous description: Faust (1997): figs 1-6.

Taxonomic remarks: Cells are small, oval to oblong in valve view (Figs 9a, b, 20a). Both the right and



Figs 9a-e. *Prorocentrum norrisianum*. 9a-e: SEM, 9a: right valve showing oval to oblong cell; 9b: left valve showing smooth thecal surface with scattered valve pores; 9c: lateral view, both the right and left valve are slightly convex and the intercalary band is smooth; 9d: the periflagellar area is small, triangular and consists of 6 platelets; the flagellar pore (F) is larger than the auxiliary pore (A) and the periflagellar area is surrounded by a wide rim (arrows); 9e: the valve surface is perforated by two different sizes of pores (arrows) seen only under high magnification. – Scale bars in Figs 9a-b: 10 μm, Figs 9c-e: 1μm.

Table 8. Comparison of cell size and morphological features in *Prorocentrum norrisianum*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 14-18, W: 10-12	L: 20-25, W: 13-16 (Faust 1997)
Cell shape	Oval to oblong	Oval with straight side (Faust 1997)
Valve pores (Vp) D=diameter (μm)	Two different sizes Vp: 45-84, D: 0.05-0.14	Two different sizes (Faust 1997) Vp: 95-105 (Faust 1997)
Marginal pores	Absent	Absent (Faust 1997)
Periflagellar area	Rim around periflagellar area 6 platelets	Left valve margin with distinctly marked collar (Faust 1997) 8 platelets (Faust 1997)
Intercalary band	Smooth	Smooth (Faust 1997)
Pyrenoid	No data	Present (Faust 1997)

left valve are slightly convex (Fig. 9c). The cell measures 14 - 18 μm (16 ± 1.8 μm) in length and 10 - 12 μm (10 ± 1.2 μm) in width (n = 5 cells). The thecal surface is smooth, and two different sizes of pores are scattered on the surface (Figs 9a, b, e, 20b). The pores can only be seen under high magnification (× 10 000). They have smooth edges and are located closer together towards the periphery of the cell (Figs 9b, e). The pore diameter is 0.05 - 0.14 μm. Approx. 45 - 84 pores are present on each valve. The periflagellar area is small, triangular and surrounded by a wide rim. It consists of 6 platelets (Fig. 9d). The flagellar pore is larger than the auxiliary pore (Fig. 9d). No ornamentations are present in the periflagellar area (Fig. 9d). The left valve is slightly convex anteriorly (Figs 9a, c). The intercalary band is smooth (Fig. 9c). It is narrow in newly-formed cells but becomes wider in older cells.

According to Faust (1997), *P. norrisianum* is a photosynthetic species with golden-brown chloroplast, a central pyrenoid and the nucleus at the posterior end. The cells are delicate and easily damaged under high-resolution microscopy.

The description of *P. norrisianum* from Malaysia fits with the original description by Faust (1997). Only, the material from Malaysia is smaller in size and has fewer valve pores and platelets in the periflagellar area (Table 8).

Observation: This species was identified only in preserved samples collected from seagrass in Sipadan Island and from *Padina* sp. in Tanjung Datu.

Previous record: It was found from floating mangrove detritus in Twin Cays, Belize (Faust 1997).

Toxicology: Unknown

Figs 10a-i. *Prorocentrum rhathymum*. 10a, b: Light micrographs (DIC) showing oval to oblong cells; 10a: cell with golden-brown chloroplast, central pyrenoid (arrow) and wing-like structure apically (arrowhead); 10b: cell with posterior nucleus (N); 10c, d: epifluorescence microscopy; 10c: cell outline; 10d: valve pores; 10e-i: SEM; 10e: right valve with smooth thecal surface and valve pores radially arranged perpendicular to the valve edge; 10f: left valve with slightly concave anterior end; 10g: both valves are convex and the intercalary band is smooth; 10h: the periflagellar area is small and V-shaped. Two wing-like structures are present (arrows); 10i: two different sizes of pores are present (arrows). – Scale bars in Figs 10a-f: 10 μm, Figs 10g-i: 1μm.

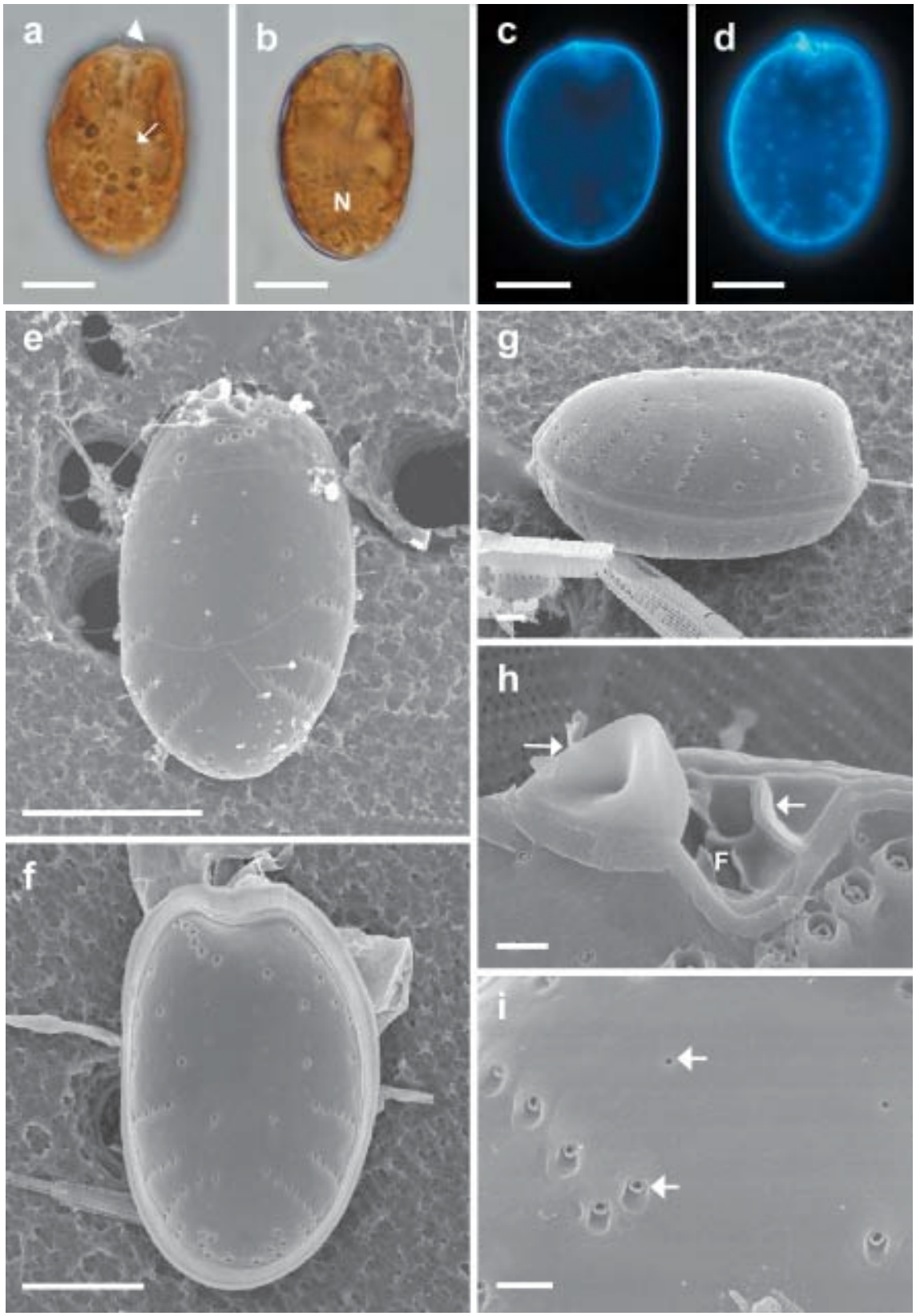

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Table 9. Comparison of cell size and morphological features in *Prorocentrum rhathymum*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 28-33, W: 18-23	L: 32-29, W: 20-22 (Loeblich et al. 1979a) L: 38-40, W: 22-25 (Fukuyo 1981)
Cell shape	Oval to oblong	Oval (Loeblich et al. 1979a, Fukuyo 1981)
Valve pores (Vp) D=diameter (μm) Small pores (Sp) Large pores (Lp)	Two different sizes Sp: 30-42, D: 0.07-0.16 Lp: 46-51, D: 0.12-0.24	Two different sizes (Loeblich et al. 1979a, fig. 11)
Trichocyst pores (Tp)		Tp: c. 80 (Loeblich et al. 1979a)
Marginal pores	Absent	Not mentioned (Loeblich et al. 1979a, Fukuyo 1981)
Periflagellar area	Two wing-like structures	Apical spine (Loeblich et al. 1979a) Small anterior spine with wing (Fukuyo 1981)
	c. 7 platelets	7-8 platelets (Fukuyo 1981)
Intercalary band	Smooth	Not mentioned (Loeblich et al. 1979a, Fukuyo 1981)
Pyrenoid	Present	Not mentioned (Loeblich et al. 1979a, Fukuyo 1981)

Prorocentrum rhathymum Loeblich III, Sherley et Schmidt 1979

Figs 10a-i, 21a, b.

Previous descriptions: Loeblich et al. (1979a): figs 8-13; Fukuyo (1981): figs 5-7, 47.

Taxonomic remarks: Prorocentrum rhathymum is a photosynthetic species with a golden-brown chloroplast, a posterior nucleus and a central pyrenoid (Figs 10a, b). Cells are oval to oblong in valve view (Figs 10a - f, 21a) and both valves are convex in lateral view (Fig. 10g) (Loeblich et al. 1979a). Cells measure 28 - 33 μm (30 ± 1.3 μm) in length and 18 - 23 μm (20 ± 1.8 μm) in width (n = 25 cells). The thecal surface is smooth and perforated by pores of two different sizes (Figs 10e – g, i, 21b). The small pores are scattered on the valve surface, sometimes in groups of 2 to 6, with a smooth ring (Fig. 10i). The pore diameter is 0.07 - 0.16 μm and approx. 30 - 42 pores are present on each valve. The larger pores are situated in deep depressions, radially arranged and perpendicular to the valve margin (Figs 10d - g, i). A few pores occur scattered elsewhere (Figs 10e, f). Approx. 46 - 51 of these pores are present on each valve and their diameter is 0.12 - 0.24 μm. The periflagellar area is small and V-shaped. It consists of approx. 7 platelets and is ornamented with 2 wing-like structures of different size (Fig. 10h). In the light microscope, the wing appears as a spine (Fig. 10a), as described by Loeblich et al. (1979a) and Fukuyo (1981). The anterior end of the left valve is slightly concave (Fig. 10f). The intercalary band is smooth (Fig. 10g). The margin is narrow in newly formed cells but becomes wider in older cells.

In culture, the cells may swim actively or remain embedded in mucus. This mode of living indicates that *P. rhathymum* is tychoplanktonic.

Cells of *P. rhathymum* from Sabah differ from the original description by Loeblich et al. (1979a) in being slightly smaller and possessing a pyrenoid (Table 9).

For some time this species was considered a synonym of *P. mexicanum* (e.g. Faust et al. 1999, Hansen et al. 2001, Faust & Gulledge 2002). Recently, Cortés-Altamirano and Sierra-Beltrán (2003) suggested reinstatement of *P. rhathymum* based on cell shape, microornamentation of the valve surface, habitat and biogeography. Although the material from Sabah clearly belongs to *Prorocentrum rhathymum* it also possesses some characters of *P. mexicanum* such as

trichocyst pores on both valves, a central pyrenoid and a posterior nucleus.

Observations: This species was found regularly in samples collected from Lahad Datu, Mantanani Island, Bak-Bak Beach, Mabul Island, Tunku Abdul Rahman Park, Sipadan Island and Tanjung Datu. It was associated with *Padina* spp., *Sargassum* spp., dead coral and seagrasses.

Previous records: Prorocentrum rhathymum was first collected from a surface water sample at the Virgin Island (Loeblich et al. 1979a) and subsequently from macroalgae in coral reefs of New Caledonia and Ryukyu Islands (Fukuyo 1981).

Toxicology: A bioassay test indicated that *P. rhathymum* was not toxic to *Artemia franciscana*.

Prorocentrum sculptile Faust, 1994

Figs 11a-j, 22a, b.

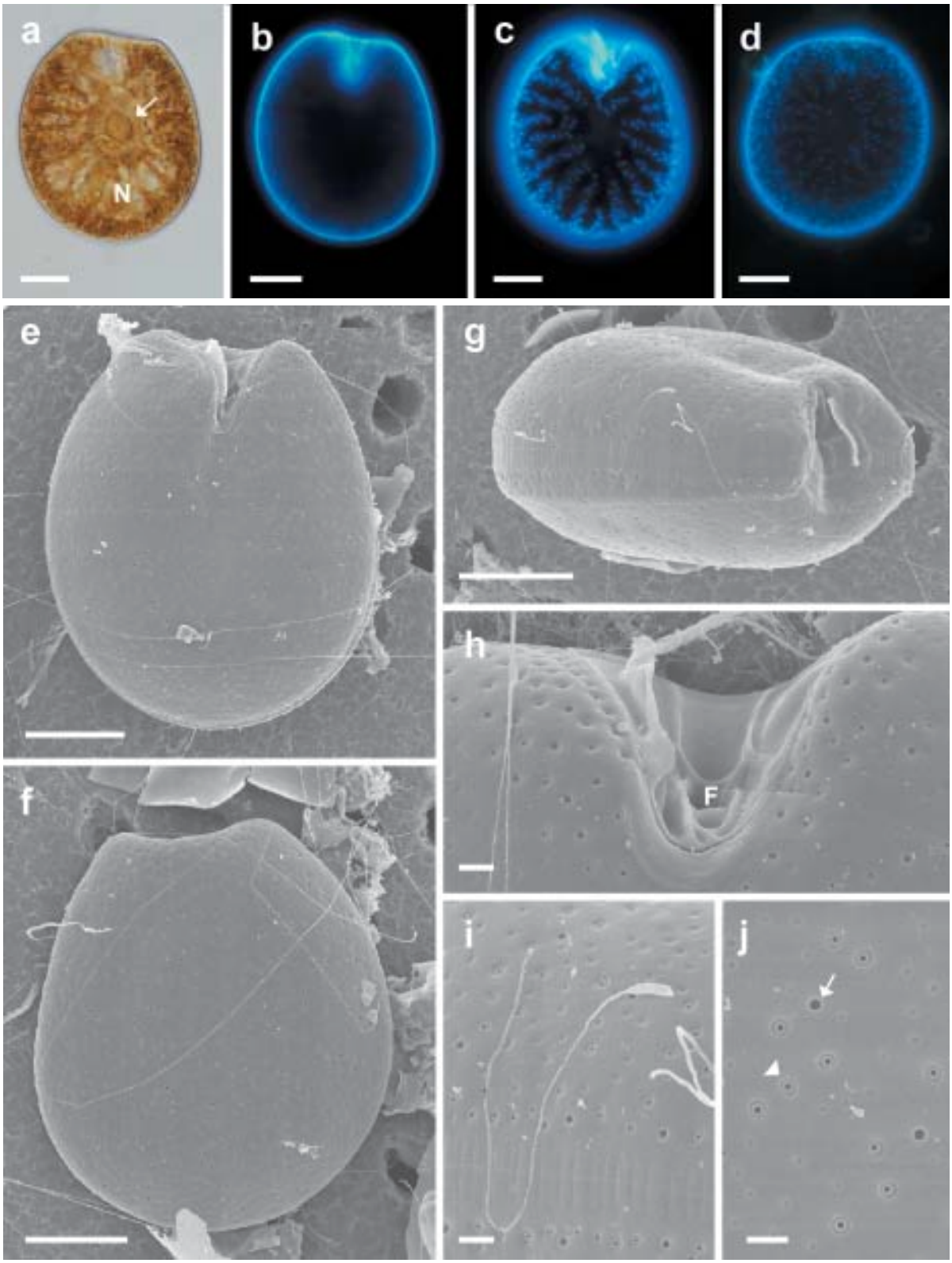
Previous descriptions: Faust (1994): figs 8-13; Hansen et al. (2001): pl. 5, fig. E & pl. 6, fig. H.

Taxonomic remarks: Prorocentrum sculptile is a photosynthetic species with golden-brown chloroplast, a central pyrenoid and a posterior nucleus (Fig. 11a). Asexual reproduction resulting in groups of 2, 4 or 8 cells was observed in culture (not shown).

Cells are round to broadly oval in valve view (Figs 11a - f, 22a). Both valves are convex in lateral view and slightly concave in the upper region of the right valve (Fig. 11g). The cell measures 40 - 48 μm (44 ± 1.5 μm) in length and 35 - 40 μm (38 ± 1.2 μm) in width in specimens isolated from Lahad Datu (n = 25 cells) and 34 - 40 μm (37 ± 1.7 μm) in length and 30 - 35 μm (32 ± 2.0 μm) in width in specimens isolated from Sipadan Island (n = 30 cells). The thecal surface has round to oblong depressions (Figs 11e - j, 22b). Pores of different sizes are present, i.e. trichocyst pores and valve pores (Figs 11j, 22b). Both types are encircled by a smooth ring-shaped edge (Fig. 11j). Approx. 45 - 84 pores per valve are present and their diameter is 0.2 - 0.3 μm. There are c. 221 - 302 trichocyst pores on each valve, each with a diameter of 0.1 - 0.2 μm. The distance between the trichocyst pores ranges from 0.5 to 2.1 μm. The pores are radially arranged from the cell margin to the centre of the cell (Figs 11c - f). Trichocyst pores are located in shallow depressions on the valve surface. Ejected trichocysts form long threads with a head-like structure (Fig. 11i). The centre of each valve lacks pores (Figs 11c - f). Marginal pores are absent.

Table 10. Comparison of cell size and morphological features in *Prorocentrum sculptile*.

Characteristics	This study	References
Cell size (μm) L=length, W=width	L: 40-48, W: 35-40 (Lahad Datu) L: 34-40, W: 30-35 (Sipadan Island)	L: 30-37, W: 30-32 (Faust 1994, Hansen et al. 2001)
Cell shape	Round to broadly oval	Broadly ovate (Faust 1994) Oval (Hansen et al. 2001)
Valve pores (Vp) D=diameter (μm) Trichocyst pores (Tp)	Two different sizes Vp: 45-84, D: 0.20-0.30 Tp: 221- 302, D: 0.10-0.20	Tp: D: 0.13 (Faust 1994) Not mentioned (Hansen et al. 2001)
Marginal pores	Absent	Not mentioned (Faust 1994, Hansen et al. 2001)
Periflagellar area	Wing-like structure Approx. 8 platelets	Thin, apical structure (Faust 1994) Small apical plate (Hansen et al. 2001) Not mentioned (Faust 1994, Hansen et al. 2001)
Intercalary band	Smooth, transversely striated	Smooth (Faust 1994, Hansen et al. 2001)
Pyrenoid	Present	Present (Faust 1994) Absent (Hansen et al. 2001)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The periflagellar area is narrow and V-shaped and composed of approx. 8 platelets (Fig. 11h). The flagellar pore is surrounded by a flange (Fig. 11h). The periflagellar area is half obscured by a wing-like structure (Figs 11c, e, g, h). The left valve is concave anteriorly (Fig. 11f). The intercalary band is smooth and transversely striated (Fig. 11g). The margin is narrow in newly formed cells but becomes wider in older cells.

A comparison with the type material from the Caribbean showed that *P. sculptile* from Lahad Datu, Sabah is larger (Table 10). It is easily misidentified as *P. emarginatum* (Hansen et al. 2001) under the light microscope due to a similar pore arrangement. The two species differ by *P. sculptile* having a round to oblong depressions on the valve surface whereas *P. emarginatum* having a smooth valve surface (Faust 1990, Faust et al. 1999).

Observations: Prorocentrum sculptile was associated with seagrasses, *Padina* spp. and *Sargassum* spp. It was found in Lahad Datu, Sipadan Island, Mabul Island, Tunku Abdul Rahman Park, Bak-Bak Beach, Sepanggar Bay and Tanjung Datu.

Previous records: Prorocentrum sculptile was first reported forming coloured sand patches at the back reef of Carrie Bow Cay, Belize (Faust 1994) and on algal turf at Réunion Island (Hansen et al. 2001).

Toxicology: A bioassay test showed that *P. scuptile* was not toxic to *Artemia franciscana*.

Prorocentrum sipadanensis Mohammad-Noor, Daugbjerg et Moestrup sp. nov.

Figs 12a-e, 23a, b.

Cellulae rotundo-ovales, 18 - 19 μm longae et 15 - 16 μm latae. Superficies valvae rugosa et ab paucis poris et poris marginalibus perforata. Area periflagellaris parva et triangularis cum 8 laminis. Vitta intercalaris horizontaliter striata. In spermatophytis marinibus epiphyticum.

Diagnosis: Cells round to oval, 18 - 19 μm long and 15 - 16 μm wide. Valve surface rugose and perforated by a few pores in addition to marginal pores. The periflagellar area small and triangular, with 8 platelets. The intercalary band is horizontally striated. Epiphytic on seagrass.
Holotype: Figs 12a - c (same cell).

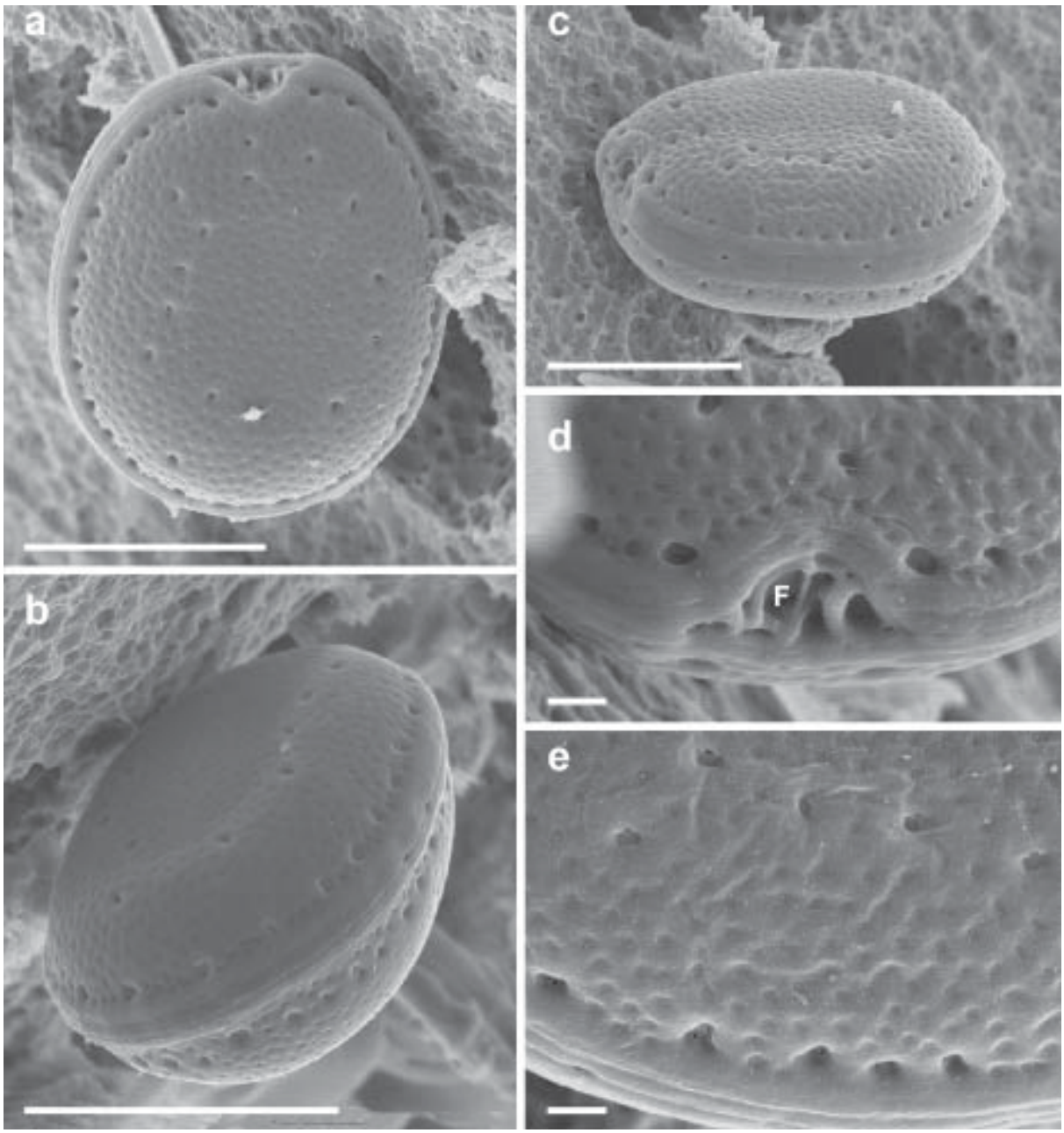
Etymology: Sipadanensis refers to the island, Sipadan Island in Malaysia where this species was found.

Descriptions: Cells are small, round to oval in valve view (Figs 12a, 23a). Both the right and left valves are flat or slightly concave in the central part (Figs 12b, c). The cell size ranges from 18 to 19 μm (18.5 ± 0.7 μm) in length and 15 to 16 μm (15.5 ± 0.7 μm) in width (n = 2 cells). The thecal plates are ornamented with round depressions (Figs 12a - e, 23b). A few deep depressions (c. 15) contain valve pores (Figs 12a - f, 23b) but the actual pores are difficult to see even at high magnification (Fig. 12e). The valve pores form a distinct pattern on the valve surface (Figs 12a - c). No pores are present in the centre of the valve (Figs 12a - c). Unevenly spaced marginal pores are also present (Figs 12a - c). The pore diameter is 0.09 to 0.10 μm (n = 3 cells) and they are present on both valves. The periflagellar area is small, triangular and consists of 8 platelets (Fig. 12d). Each platelet is lined by a flange (Fig. 12d). No apical spine is observed (Fig. 12d). The left valve is slightly convex at the anterior end (Figs 12a, d). The intercalary band is horizontally striated (Figs 12c -e).

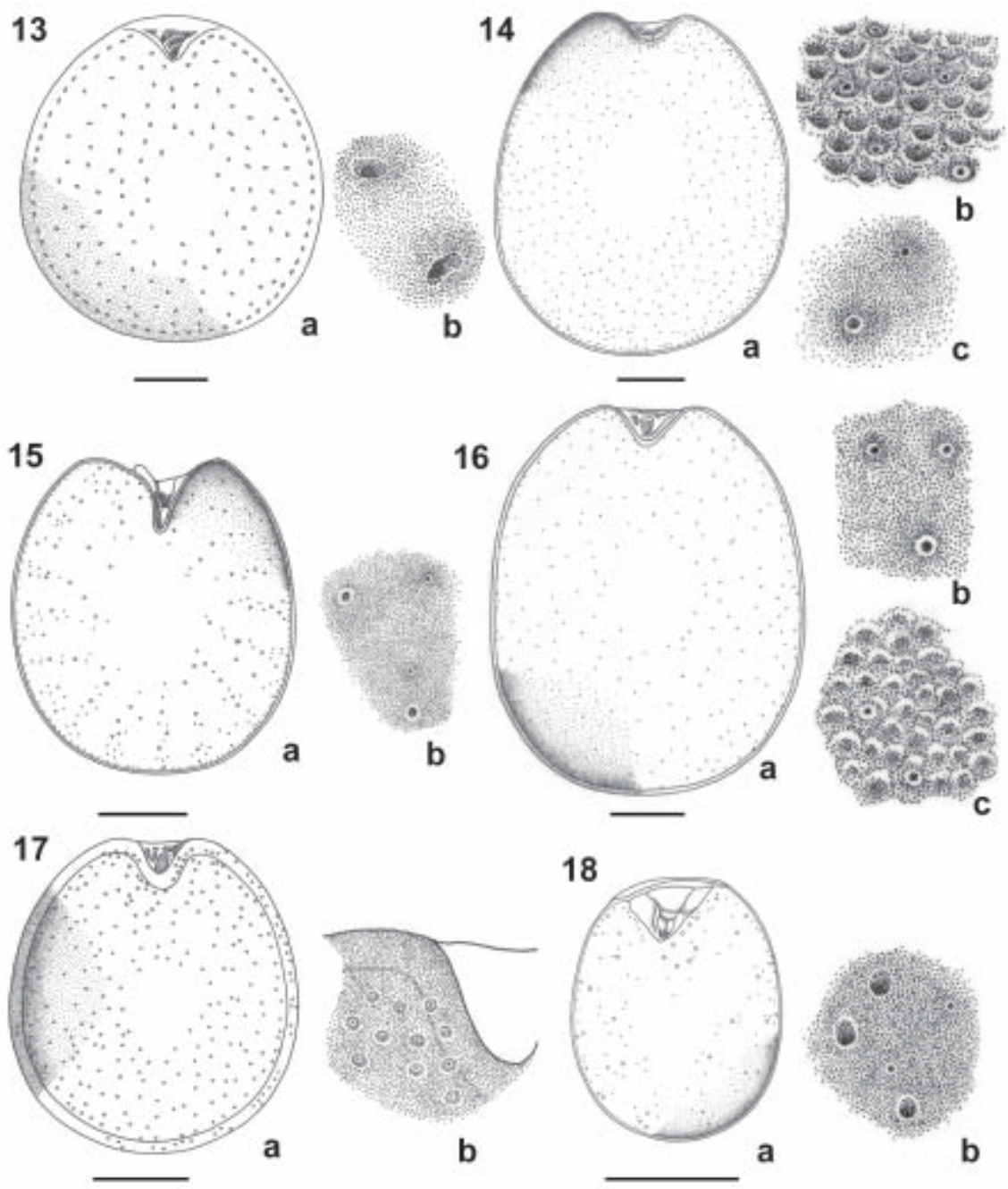
Observations: This species was observed rarely in preserved samples collected from seagrass at Sipadan Island, east Sabah.

Toxicology: Unknown

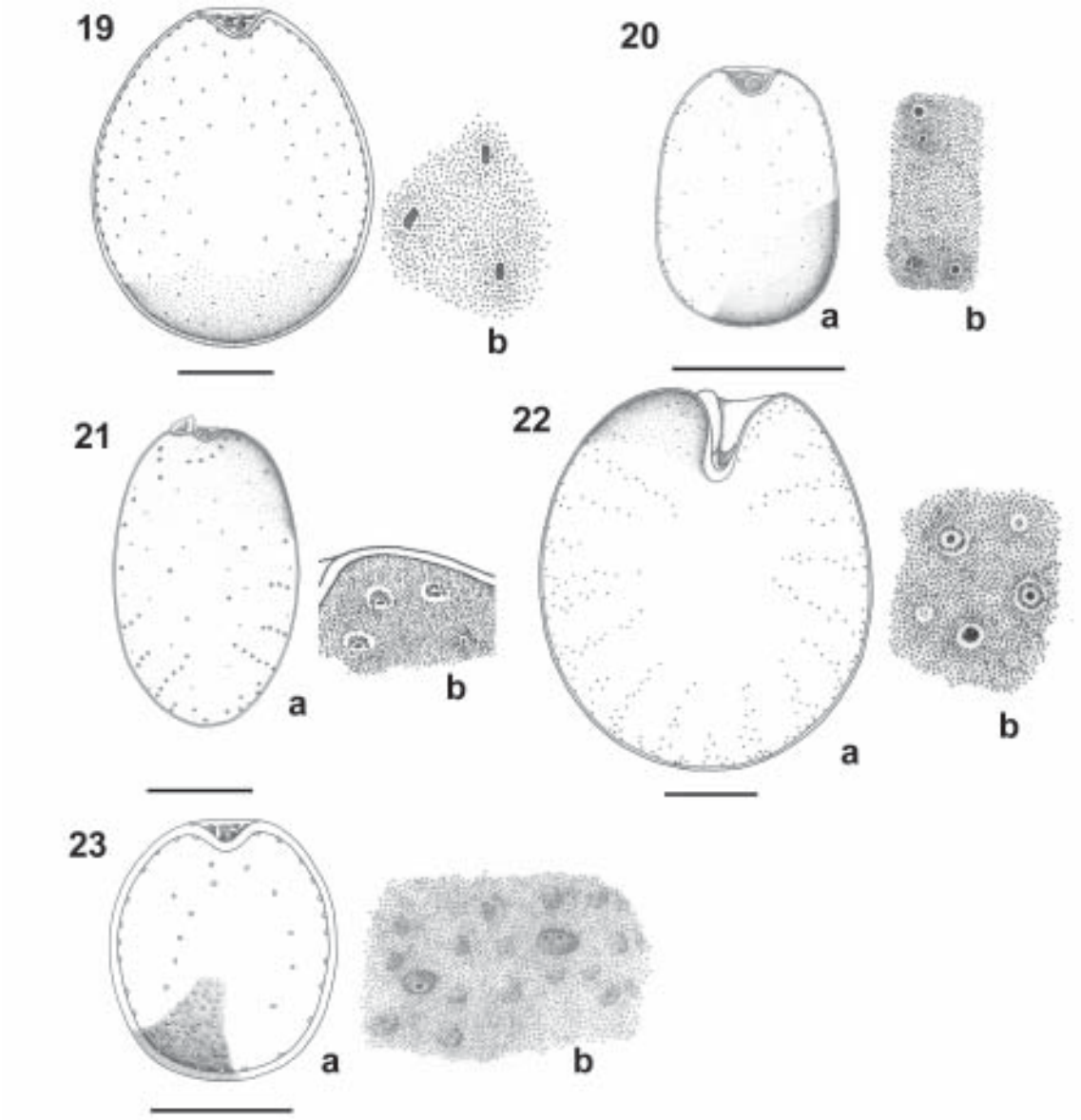
Figs 11a-j. *Prorocentrum sculptile*. 11a: Light micrograph (DIC) showing cells with golden-brown chloroplast, a central pyrenoid (arrow) and a posterior nucleus (N); 11b-d: epifluorescence microscopy; 11b: cell is round to broadly oval in valve view; 11c, d: right and left valve, respectively, with numerous valve pores in a distinct pattern; 11e-j: SEM; 11e: the right valve with scattered shallow depressions; 11f: the left valve is concave anteriorly; 11g: in lateral view, both valves are convex. The upper region of the right valve is moderately concave and the intercalary band is transversely striated; 11h: the periflagellar area is narrow V-shaped. It consists of approx. 8 platelets and is half obscured by a wing-like structure; the flagellar pore (F) is surrounded by a flange; 11i: ejected trichocyst with head-like structure; 11j: two different sizes of pores are present, i.e. valve pores (arrow) and trichocyst pores (arrowhead). – Scale bars in Figs 11a-g: 10 μm, Figs 11h-i: 1 μm.



Figs 12a-e. *Prorocentrum sipadanensis*. 12a-e: SEM; 12a. right valve showing round to oval cell, thecal surface with shallow depressions and scattered valve pores; 12b: left valve with distinct marginal pores; 12c: lateral view, both valves are convex or slightly concave in the middle, the intercalary band is horizontally striated; 12d: the periflagellar area is small and triangular; it consists of 8 platelets lined by ridges; F = flagellar pore; 12e: both valve pores and marginal pores are situated in deep depressions. – Scale bars in Figs 12a-c: 10 μm, Figs 12d-e: 1 μm.

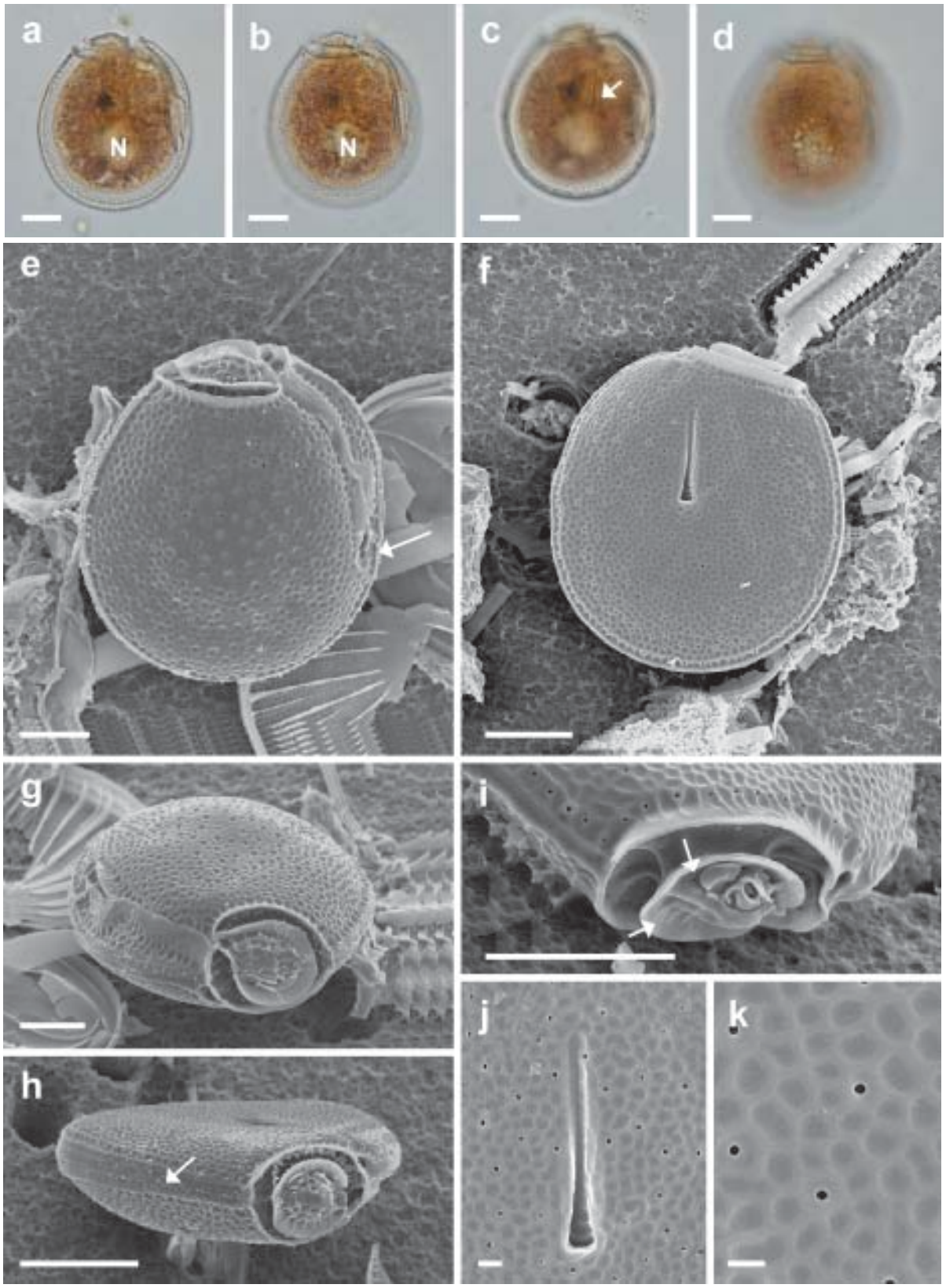


Figs 13-18. Drawings of *Prorocentrum* spp. in right valve view showing cell shape and arrangement of valve pores and marginal pores. Beside each cell is a close-up of the pores showing different sizes and shapes (not to scale). 13a: *P. arenarium* showing scattered valve pores except in the centre, and prominent marginal pores; 13b: kidney-shaped valve pores; 14a: *P. concavum* showing numerous valve pores except in the centre; 14b: side view showing rugose thecal surface with pores located in shallow depressions; 14c: top view showing two different sizes of pores; 15a: *P. emarginatum* showing radially arranged valve pores; 15b: two different sizes of pores; 16a: *P.* cf. *faustiae* showing numerous valve pores except in the middle; 16b: top view showing two different sizes of pores; 16c: side view showing rugose thecal surface with pores situated in shallow depressions; 17a: *P. foraminosum* with scattered valve pores except in the middle; 17b: valve pores are located in shallow depressions; 18a: *P. formosum* showing pores arranged in a characteristic pattern; 18b: two different sizes of pores. – Scale bars = 10 μm.



Figs 19-23. Drawings of *Prorocentrum* spp. from right valve view showing cell shape and arrangement of valve pores and marginal pores. Beside each cell is a close-up of the pores showing different sizes and shapes (not to scale). 19a: *P. lima* showing scattered valve pores except in the middle, and marginal pores; 19b: oblong to kidney-shaped valve pores; 20a: *P. norrisianum* showing scattered valve pores; 20b: two different sizes of valve pores; 21a: *P. rhathymum* showing radially arranged and scattered valve pores; 21b: two different sizes of pores; 22a: *P. sculptile* showing radially arranged pores; 22b: two different sizes of pores; 23a: *P. sipadanensis* showing a few valve pores and marginal pores; 23b: thecal surface with shallow depressions and valve pores located in deep depressions. – Scale bars = 10 μm.

Figs 24a-k. *Sinophysis canaliculata*. 24a-d: Light micrographs (DIC); 24a, b: in lateral view, cells are circular and the nucleus (N) is located posteriorly; 24c: a conspicuous narrow depression is situated in the left lateral plate (arrow); 24d: the valve surface is areolated; 24e-k: SEM; 24e: right lateral plate with long and narrow sulcus and a posterior opening where the longitudinal flagellum emerges (arrow); 24f: left lateral plate with narrow depression in the upper part; 24g: the right lateral plate is convex in apical view; 24h: the left lateral plate is slightly concave or flat in apical view; the lateral plates are joint together by the sagittal suture (arrow); 24i: the epitheca is divided into two asymmetrical plates (arrows); the cingulum is bordered by well-defined anterior and posterior lists; 24j: the narrow depression in the left lateral plate; 24k: valve pores are circular with smooth edges and situated in every two or three areolae. – Scale bars in Figs 24a-i: 10 μm, Figs 24j-k: 1 μm.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Order Dinophysiales Kofoid 1926

Species of this order are characterized by having laterally flattened cells with dinokont flagellar orientation and a premedian cingulum. Cingulum and sulcus are often lined by wide lists supported by ribs (Steidinger & Tangen 1996). Fensome et al. (1993) include three families in the order: Amphisoleniaceae Lindemann 1928, Dinophysiaceae Stein 1883 and Oxyphysaceae Sournia 1984. In the genus *Sinophysis,* family Dinophysiaceae, 6 species are known i.e. *S. microcephalus* Nie et Wang (Nie & Wang 1944, Faust 1993c), *S. ebriolum* (Herdman) Balech (Herdman 1924, Balech 1956, Hoppenrath 2000b), *S. canaliculata* Quod, Ten-Hage, Turquet, Mascarell et Couté (Quod et al. 1999), *S. stenosoma* Hoppenrath, *S. grandis* Hoppenrath (Hoppenrath 2000b) and *S. minima* Selina et Hoppenrath (Selina & Hoppenrath 2004). *Sinophysis microcephalus* and *S. canaliculata* are considered tropical species while *S. ebriolum, S. stenosoma, S. grandis* and *S. minor* are from temperate areas. All known species of *Sinophysis* are heterotrophic and lack chloroplasts. In this study, two *Sinophysis* species were identified (*S. canaliculata* and *S. microcephalus).*

Sinophysis canaliculata Quod, Ten-Hage, Turquet, Mascarell et Couté 1999

Figs 24a-k.

Previous description: Quod et al. (1999): figs 1- 16.

Taxonomic remarks: Sinophysis canaliculata has a posterior nucleus (Figs 24a, b). Cells are circular in lateral view (Figs 24a - f) and compressed laterally (Fig. 24h). The right lateral plate is convex (Fig. 24g) while the left lateral plate is slightly concave or flat (Fig. 24h). The width ranges from 42 to 46 μm (43 ± 2.1 μm) and the length from 47 to 49 μm (48 ± 2.0 μm) (n = 5 cells). The thecal surface is areolated and perforated by pores (Figs 24e, f). The areolae are more or less round to oval, and polygonal along the periphery of the cell (Figs 24e - i). Valve pores are circular with smooth edges and situated in every two to three areolae (Fig. 24k), occasionally between the areolae (not shown). The pore size ranges from 0.19 to 0.30 μm (n = 3 cells).

The epitheca is small and divided into two asymmetrical plates (Figs 24e, g - i). The ornamentation of the left epithecal plate is very complex, more so than in the right plate (Fig. 24i). The hypotheca is formed by four plates, two lateral plates (left and right) and two ventral plates (Quod et al. 1999). The lateral plates are joined together by the sagittal suture located in the centre of the megacytic zone (Fig. 24h). A narrow, long sulcus is situated on the right lateral cell side (Figs 24b, e, g). The sulcus is ornamented by lists that obscure part of the sulcal area (Fig. 24e). The length of the sulcus does not exceed two-thirds of the lateral plate length and it has an opening at the posterior end where the longitudinal flagellum emerges (Fig. 24e). An elongate and narrow depression is located on the upper part of the left lateral plate (Figs 24c, f, h, j). It is 12 μm long (n = 5 cells) and can be observed also under the light microscope (Fig. 24c). The function of this structure is unknown (Quod et al. 1999). The cingulum is narrow and rounded with well-defined anterior and posterior lists. It has fewer pores (Figs 24e - i).

This species differs from *S. microcephalus* mainly in the shape of the cell and the presence of the depression on the left lateral plate.

Observation: Sinophysis canaliculata was observed in preserved samples from Tunku Abdul Rahman Park associated with *Sargassum* spp and *Padina* spp.

Previous record: This species is presently known only from coral reefs at St. Leu, Réunion Island (Quod et al. 1999).

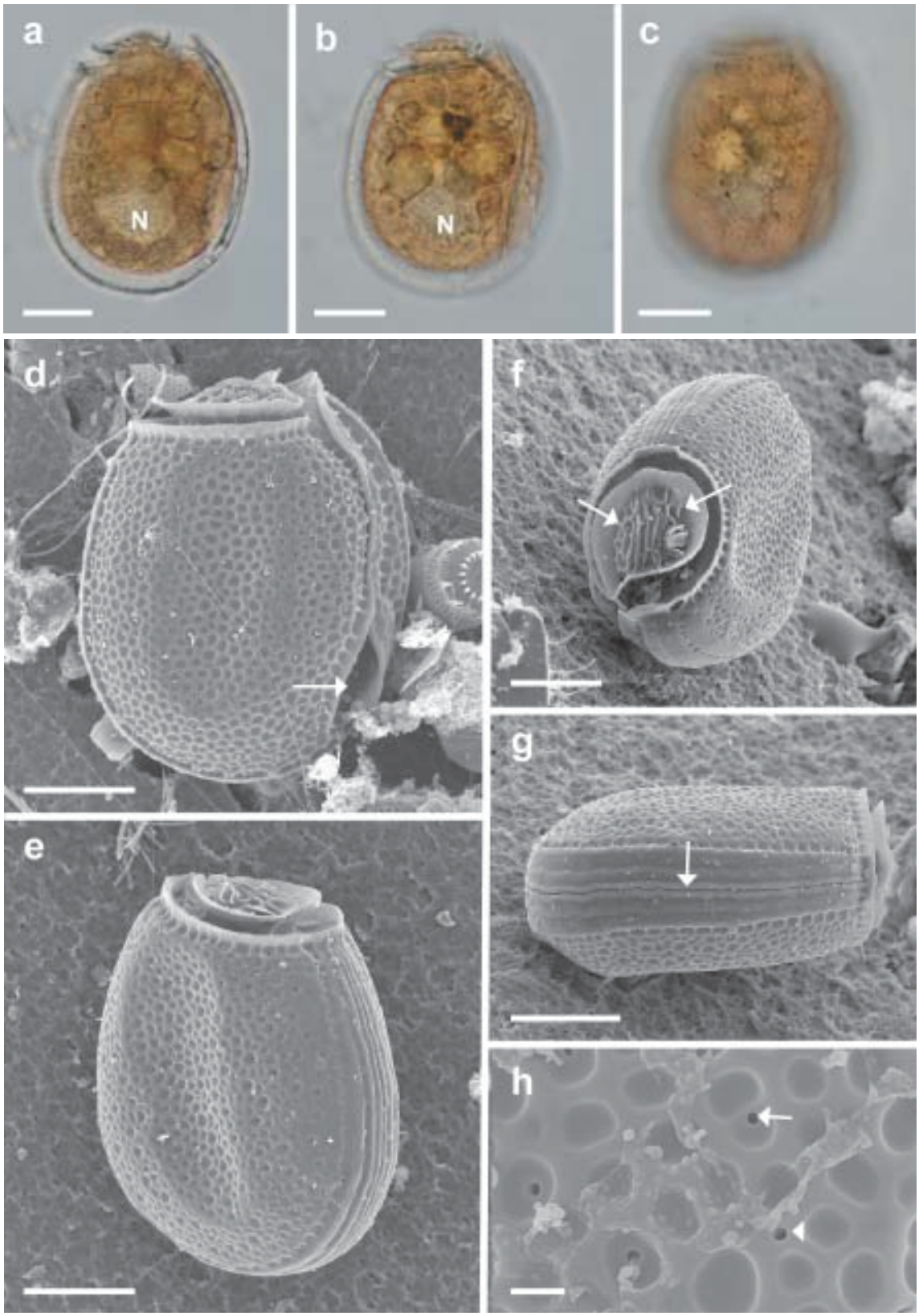
Toxicology: Unknown.

Sinophysis microcephalus Nie et Wang 1944

Figs 25a-h.

Previous descriptions: Nie & Wang (1944): figs 1-8; Faust (1993c): figs 1-11.

Figs 25a-h. *Sinophysis microcephalus*. 25a-c: Light micrographs (DIC); 25a, b: in lateral view, cells are elongate and the nucleus (N) is located posteriorly; 25c: the thecal surface is areolated; 25d-h: SEM; 25d: the right lateral plate with long and narrow sulcus extending along the entire length of the plate; it has a posterior opening where the longitudinal flagellum emerges (arrow); 25e: the left lateral plate showing polygonal areolae along the cell margin; 25f: the cell is compressed laterally and the epitheca is divided into two asymmetrical plates (arrows); 25g: the lateral plates are merged together by the sagittal suture located in the centre of the megacytic zone (arrow); 25h: valve pores are circular with smooth edges, and situated between the areolae (arrowhead) or in the areolae (arrow). – Scale bars in Figs 25a-g: 10 μm, Fig. 25h: 1 μm.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Taxonomic remarks: Sinophysis microcephalus has a posterior nucleus (Figs 25a, b). Cells are elongate with a round posterior end (Figs 25a - e) and compressed laterally (Figs 25f, g). The width ranges from 29 to 32 μm (30 ± 1.3 μm) and the length from 36 to 38 μm (37 ± 0.8 μm) (n = 5 cells). The thecal surface is areolated (Figs 25c - e). The areolae are round to oval and often perforated by pores (Figs 25d, e, h). Along the cell margin, the areolae are polygonal (Figs 25d - g). Valve pores are circular, smooth edged and located in every two or three areolae (Fig. 25h). Some valve pores are located between the areolae (Fig. 25h). The pore size ranges from 0.15 to 0.28 μm.

The epitheca comprises two asymmetrical plates (Fig. 25f). The left epitheca plate is more complex than the right one in both ornamentation and shape (Fig. 25f). The hypotheca comprises four plates i.e. two lateral plates (left and right) and two ventral plates (Nie & Wang 1944, Faust 1993c). The lateral plates are merged together by the sagittal suture located in the centre of the megacytic zone (Fig. 25g). On the right lateral side there is a long, narrow sulcus (Figs 25b, d), which is lined by a prominent list that partly obscures the sulcal area (Fig. 25d). The sulcus is almost as long as the hypotheca and it has a wide opening at the posterior end where the longitudinal flagellum emerges (Fig. 25d). The cingulum is narrow, has only a few pores and is surrounded by well-defined anterior and posterior lists (Fig. 25f).

Observations: Sinophysis microcephalus was observed in preserved samples from *Sargassum* spp., *Padina* spp., seagrasses and dead coral. The samples were collected from Bak-Bak Beach, Tunku Abdul Rahman Park, Mabul Island and Sipadan Island.

Previous records: This species was first observed in a surface water collection from Shintsuen Kong, Hainan Region, in the South China Sea (Nie & Wang 1944). Later, it was found in floating detritus at Twin Cays, Belize (Faust 1993c). *Sinophysis microcephalus* is a tropical, benthic dinoflagellate.

Toxicology: Unknown.

Order Gonyaulacales F. J. R. Taylor 1980

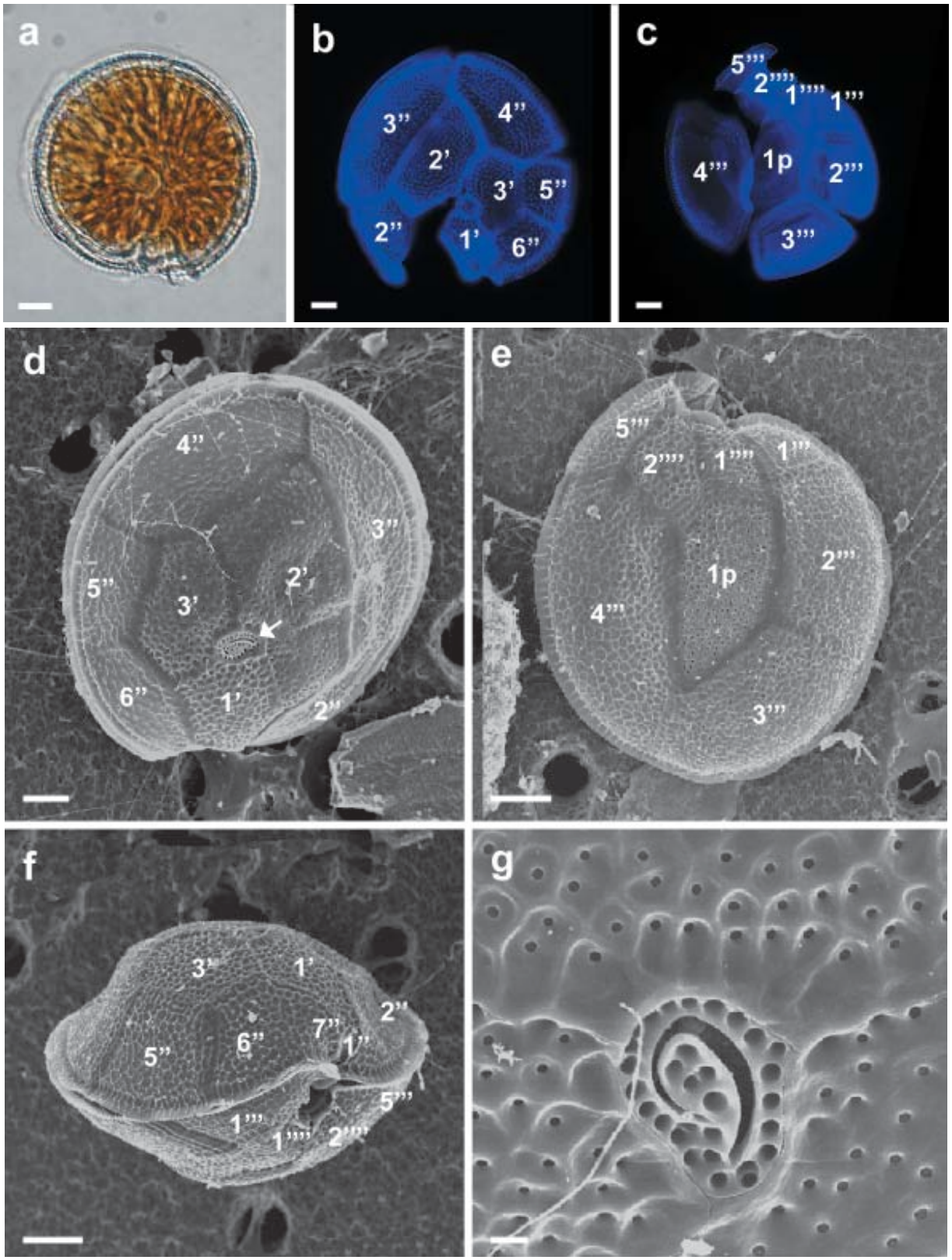
Gonyaulacalean tabulation is typically characterized by an asymmetrical apical pore complex, four apical plates of which the midventral first apical plate is asymmetrical, no anterior intercalary plates, six precingular plates, six cingular plates, six postcingular plates, one posterior intercalary plate, one antapical plate and five sulcal plates (Fensome et al. 1993). The order comprises fourteen families. In this study, 5 epiphytic species from *Gambierdiscus, Coolia* and *Ostreopsis* were identified. They are classified in the family Goniodomaceae Lindemann 1928, subfamily Gambierdiscoideae Fensome et al. (1993). The most distinctive feature of gambierdiscoideans is the anterior-posterior compression of the motile, photosynthetic cell (Fensome et al. 1993).

In the genus *Gambierdiscus*, six species have been described viz. *G. toxicus* Adachi et Fukuyo (Adachi & Fukuyo 1979), *G. belizeanus* Faust (Faust 1995), *G. yasumotoi* Holmes (Holmes 1998), *G. pacificus* Chinain et Faust, *G. australes* Faust et Chinain and *G. polynesiensis* Chinain et Faust (Chinain et al. 1999). The plate formula is Po, 3', 7", 6C, 8S, 5'", 1p, 2'"" (Chinain et al. 1999). *Gambierdiscus toxicus* has been extensively studied after being confirmed producer of ciguateric toxins (Bagnis et al. 1980, Durand-Clement 1987). Other species of *Gambierdiscus* are also known to produce ciguatoxin-like toxin and maitotoxin (Holmes 1998, Chinain et al. 1999). In *G. belizeanus* toxin production is unknown.

The genus *Coolia* can be distinguished from other species of the family Goniodomataceae by its smaller size and oval shape. It is slightly compressed anterior-posteriorly, the cingulum is descending, the epitheca is smaller than the hypotheca and the plate formula is Po, 3', 7", 6-7C, 6-8(?)S, 5'", 2'"". Three species have been identified viz. *C. monotis* Meunier (Meunier 1919), *C. tropicalis* Faust (Faust 1995) and *C. areolata* Ten-Hage, Turquet, Quod et Couté (Ten-Hage et al. 2000c).

Species of the genus *Ostreopsis* are compressed anterior-posteriorly. Cells are tear-shaped and taper posteriorly, the cingulum is not descending and the epitheca is not noticeably smaller than the hypotheca in apical view (Steidinger & Tangen 1996).

Figs 26a-g. *Gambierdiscus pacificus*. 26a: Light micrograph (DIC) of cell with golden-brown chloroplasts; 26b, c: epifluorescence micrographs of epitheca (reversed image compared to Fig. 26d) and hypotheca, respectively; 26d-g: SEM; 26d, e: cells are oval to ellipsoidal; the thecal surface is perforated by numerous pores; 26d: epithecal view; Po is situated almost in the centre (arrow); 26e: hypothecal view; 1p is narrow and occupies about 20% of the hypotheca; 26f: ventral view; the cell is compressed anterior-posteriorly; 26g: the Po has a fish-hook-shaped opening and comprises of *c.* 30 round pores. – Scale bars in Figs 26a-e: 10 μm, Fig. 26g: 1 μm.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Nine *Ostreopsis* species are known: *O. siamensis* Schmidt (Schmidt 1902), *O. ovata* Fukuyo, *O. lenticularis* Fukuyo (Fukuyo 1981), *O. heptagona* Norris, Bomber et Balech (Norris et al. 1985), *O. mascarenensis* Quod (Quod 1994), *O. labens* Faust et Morton (Faust & Morton 1995), *O. marinus* Faust, *O. belizeanus* Faust and *O. caribbeanus* Faust (Faust 1999). The general plate tabulation for *Ostreopsis* is Po, 3', 7", 6C, 6S(?), Vp, Rp, 5'", 1p, 2'"" (Faust & Morton 1995, Faust et al. 1996, Faust 1999). The plate tabulation once have been suggested as 1pp, 4', 6", 6c, 8s, 5'" and 2'"" by Besada et al. (1982). They agreed with the placement of the genus in the Order Gonyaulacales but argued that the first apical plate had been displaced by Schmidt (1902) and Fukuyo (1981) as first precingular plate. This is because if *Ostreopsis* spp. has gonyaulacoid affinities, they should have four apical plates, the ventral pore positioned on the right hand margin of the first apical plate and the precingular plate usually does not completely encircle the cell. The few studies on *Ostreopsis* (Faust & Morton 1995, Faust et al. 1996) have shown that these species are mixotrophic. Samples from natural populations were found to contain food particles (centric diatoms, ciliates and small microalgae) and it has been suggested that the ventral pore (Vo) functions as port of entry for the food particles (Faust et al. 1996).

Gambierdiscus pacificus Chinain et Faust 1999

Figs 26a-g.

Previous descriptions: Chinain et al. (1999): figs 11-13.

Taxonomic remarks: Gambierdiscus pacificus has golden-brown chloroplasts (Fig. 26a) and a posteriorly situated nucleus (Chinain et al. 1999). Cells are oval to ellipsoidal in apical view (Figs 26a, d) and compressed anterior-posteriorly (Fig. 26f). Cells range in size from 59 to 63 μm (61 ± 1.5 μm) in length and from 53 to 58 μm (55 ± 2.0 μm) in width (n = 5 cells). The thecal surface is perforated by numerous, smooth-edged pores (Figs 26d - g).

The plate formula is Po, 3', 7", 6C, 8S, 5'", 1p, 2'"" (Chinain et al. 1999). The Po has a fish-hook-shaped opening, c. 30 round pores (Fig. 26g) and is positioned almost in the centre of the epitheca (Fig. 26d). The apical plates 1' and 3' are small compared to apical plate 2' (Figs 26b, d). Plate 2' is narrow and rectangular. In the precingular series, plate 3" is the longest, plate 4" is medium-sized and plates 1", 2", 5", 6" and 7" are small (Fig. 26d). The cingulum is deeply excavated, ornamented with a prominent list (Figs 26d - f). The sulcus has a small and deep opening (Fig. 26f). Postcingular plates 2'", 3'" and 4'" are larger than 1'" and 5'" (Fig. 26e). Plate 1p is narrow (Fig. 26e). Plates 1'"" and 2'"" are small and located on the ventro-anterior side of the hypotheca (Figs 26e, f).

Observations: This species was found in Kota Kinabalu and Sipadan Island associated with *Sargassum* sp. and seagrasses.

Previous records: Gambierdiscus pacificus was described from red algae, *Jania* sp. and *Amphiroa* sp. at Hao Island, Tuamotu Archipelago, and in the plankton at Cat Cay and Manatee Cay, Belize, Central America (Chinain et al. 1999). See further in the discussion.

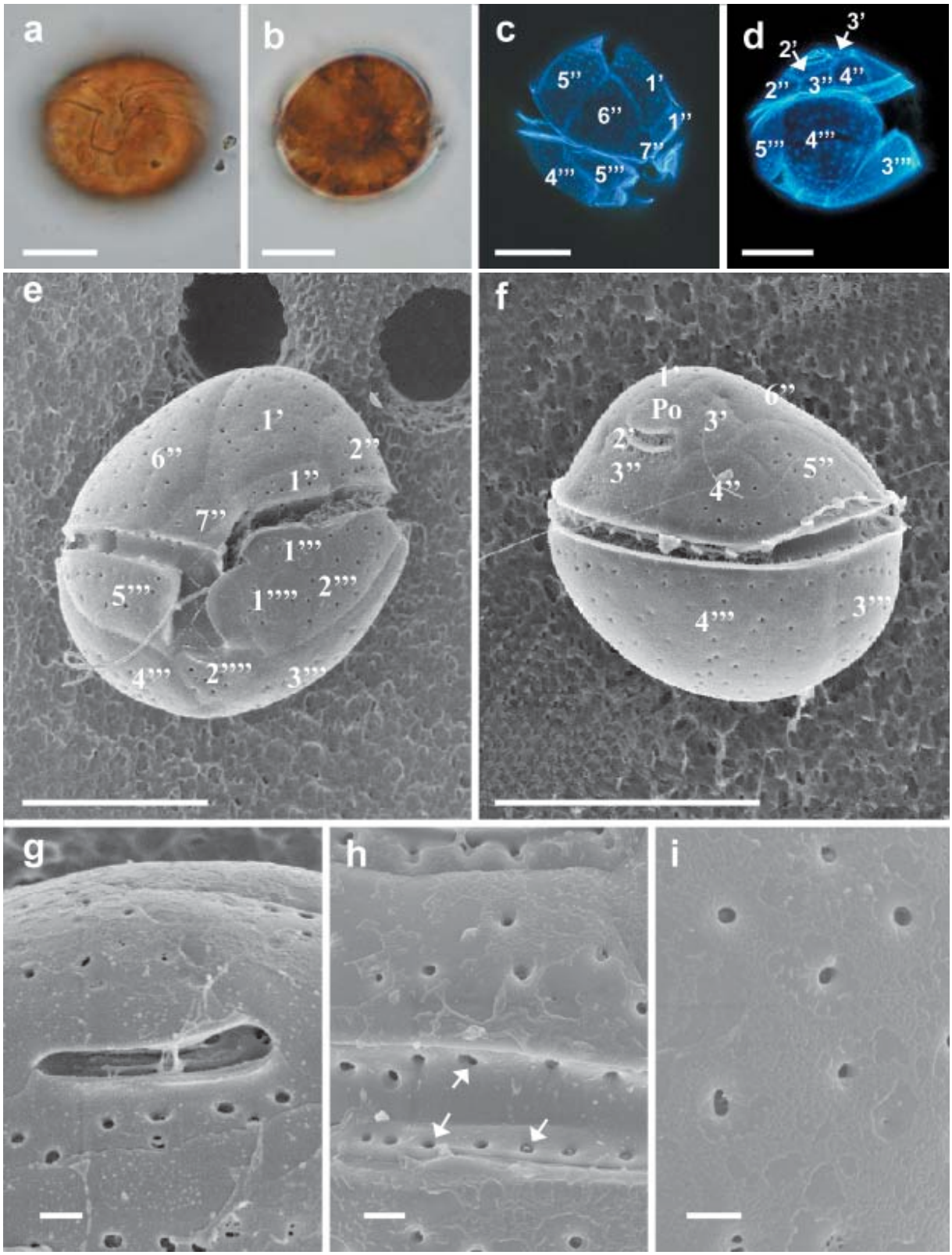
Toxicology: Bioassay tests revealed that *G. pacificus* from Kota Kinabalu was not toxic to *A. franciscana,* whereas *G. pacificus* from Sipadan Island was toxic to *A. franciscana*. The dichloromethane soluble fraction of *G. pacificus* has been reported to have ciguatoxin-like activities (Chinain et al. 1999).

Coolia sp.

Figs 27a-i.

Taxonomic remarks: Coolia sp. has golden-brown chloroplasts (Figs 27a, b). Cells are almost spherical in ventral view (Figs 27a, b, e, f). The hemispherical epitheca is slightly smaller than the hemispherical hypotheca (Figs 27e, f). The cell size ranges from 21 to 24 μm (23 ± 1.1 μm) in length and 21 to 24 μm (23 ± 1.5 μm) in width (n = 5 cells). The thecal surface is smooth with scattered round to oblong

Figs 27a-i. *Coolia* sp. 27a, b: Light micrographs (DIC) of ventral and dorsal view showing golden-brown chloroplasts; 27c, d; epifluorescence micrographs; 27c: ventral view; 27d: dorsal view; 27e-i: SEM; 27e, f: cells are almost spherical and the epitheca is slightly smaller than the hypotheca; the thecal surface is smooth with scattered valve pores; 27e: ventral view; 27f: dorsal view with Po situated off centre; 27g: Po is slightly curved; it has a slit and a few pores; 27h: the cingulum is excavated with approx. 2 rows of pores (arrows); 27i: valve pores are round to oblong with smooth edges. – Scale bars in Figs 27a-f: 10 μm, Figs 27g-i: 1 μm.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pores (Figs 27e, i). The pores have smooth edges with the diameter ranging between 0.18 and 0.50 μm. The epitheca consists of 11 plates viz. a pore plate (Po), 3 apical plates and 7 precingular plates (Figs 27c - f). The plates are arranged in an irregular pattern (Figs 27e, f). The Po is located in the second apical plate (2') off centre in the epitheca. It is slightly curved, 4 to 6 μm in length and comprises a small slit and a few pores (Fig. 27g). The first apical plate (1') is wide and lies adjacent to Po/2', 3', 1", 2", 6" and 7" (Figs 27c, e, f). Among the plates in the epitheca, 1" is the smallest and 6" is the largest. The cingulum is deeply excavated, equatorial, and bordered by narrow smooth-edged lists. There are generally 2 rows of pores inside the cingulum (Fig. 27h). The sulcus is deep and partially covered by a wing-like structure projecting from 1'"" and 5'" (Fig. 27e). The posterior end of the sulcus is sometimes covered with a small extension from 2'"". The hypotheca consists of 7 plates, viz. 5 postcingular plates and 2 antapical plates (Figs 27c - f). The postcingular plates are large and occupy most of the hypotheca (Figs 27d, f). Plates of the antapical series are small but make contact with the sulcus (Figs 27c, e).

Observation: This species was found regularly in Port Dickson, Sepanggar Bay, Bangi Island, Mabul Island, Sipadan Island, Bak-Bak Beach, Tunku Abdul Rahman Park and Tanjung Datu, associated with *Sargassum* spp., *Padina* spp., dead coral, sand and seagrasses.

Toxicology: Bioassay tests on seven strains of *Coolia* sp. collected from Peninsula Malaysia, Sabah and Sarawak showed that 6 strains were toxic and one strain was non-toxic to *A. franciscana*.

Ostreopsis labens Faust et Morton 1995

Figs 28a-i.

Previous descriptions: Faust & Morton (1995): figs 1-15; Faust et al. (1996): figs 39-45.

Taxonomic remarks: Ostreopsis labens has a golden-brown chloroplast and a posterior nucleus (Fig. 28a). Cells are broadly oval in epithecal view. The cell is anterior-posteriorly compressed (Fig. 28f). The cell size ranges from 50 to 73 μm (59 ± 6.9 μm) dorsoventrally and 40 to 65 μm (51 ± 6.9 μm) in transdiameter (n = 25 cells). The thecal surface is smooth and perforated by numerous pores (Figs 28d - i), which can be seen under the light microscope. Two different sizes of valve pores are observed. The large pores are numerous whereas the number of small valve pores is low. Both pore types have smooth edges and are unevenly spaced on the valve surface (Fig. 28i). The diameter of the larger pore ranges from 0.2 to 0.5 μm, and approx. 217 to 343 pores are present on each valve.

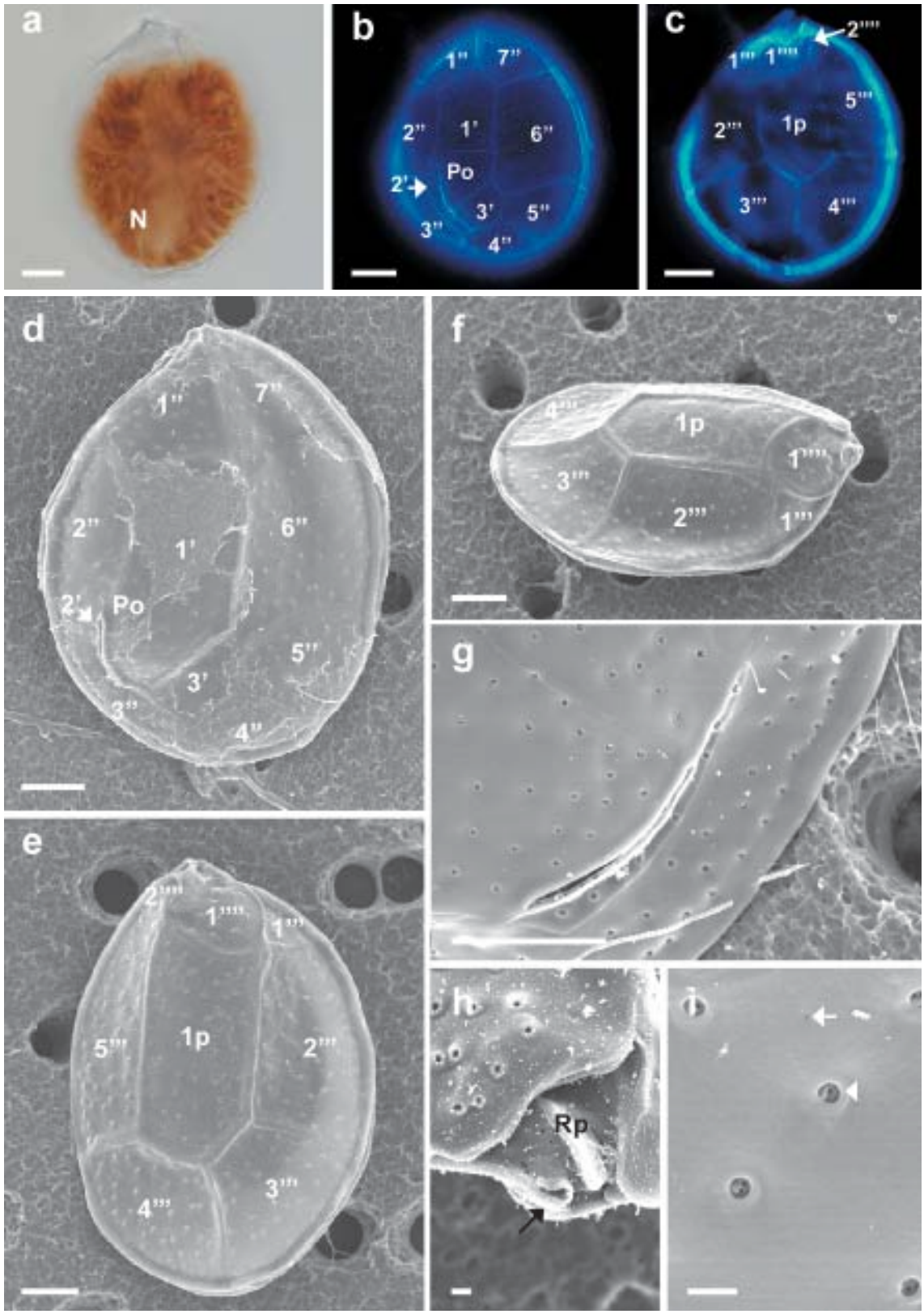
The plate formula is Po, 3', 7", 6C, 6S?, Vp, Rp, 5'", 1p and 2'"" (Faust & Morton 1995). The first apical plate (1') is long and situated almost in the middle of the epitheca (Fig. 28d). Plate 2' is small and narrow (Fig. 28d). The Po is curved, narrow, situated off centre and 14 ± 1.2 μm long (n = 5) (Figs 28d, g). This plate was considered to be associated with plate 2' by Faust et al. (1995). Plate 3' is medium-sized and triangular (Fig. 28d). Precingular plate 6" is the largest plate in the epitheca (Fig. 28d).

The cingulum is excavated and bordered by lists (Fig. 28f). The ventral plate (Vp) with the ventral pore (Vo) is situated in the cingulum (Fig. 28h, arrow). A curved ridged plate (Rp) is positioned above Vo (Fig. 28h). The postcingular plate 1'"is small while plates 2'", 3'", 4'" and 5'" are larger (Fig. 28e). Antapical plates 1'"" and 2'"" are small and located at the ventral part of the cell (Fig. 28e). Plate 1p is long, medium-sized and touches plates 1'", 2'", 3'", 4'", 5'" and 1'"" (Fig. 28e).

The morphological description of *O. labens* from Malaysia generally fits the original description of Faust & Morton (1995). The Malaysian material differs in having two sizes of pores, smaller cell size and a shorter Po.

Observations: This species was associated with *Sargassum* spp., *Padina* spp. and seagrasses. It was found in samples collected from Sipadan Island, Mabul Island, Tunku Abdul Rahman Park, Sepanggar Bay and Tanjung Datu.

Figs 28a-i. *Ostreopsis labens*. 28a: Light micrograph (DIC) of cell showing golden-brown chloroplast and nucleus (N); 28b, c: epifluorescence micrographs, cells in epithecal and hypothecal view (reversed image compared to Fig. 28e), respectively; 28d-i: SEM; 28d, e: cells are broadly oval and the thecal surface is perforated by numerous pores; 28d: epithecal view with Po situated off centre; plate 1' is long and 7-sided; 28e: hypothecal view with the long 1p; 28f: side view; the cell is anterior-posteriorly compressed; 28g: Po is curved and narrow; 28h: ventral view, the ventral plate has a pore (arrow), and a ridged plate (Rp) is also visible; 28i: two different sizes of valve pores are present (arrow and arrowhead). – Scale bars in Figs 28a-g: 10 μm, Figs 28h-i: 1 μm.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Previous records: Ostreopsis labens has been reported from the water column and from sand in Belize, associated with macroalgae of Oshigaki and Iriomote Island, Japan (Faust & Morton 1995) and from warm tropical waters in the East China Sea, Southwest Indian Ocean and the Caribbean Sea (Faust et al. 1996).

Toxicology: A bioassay test revealed that *O. labens* was toxic to *A. franciscana*.

Ostreopsis lenticularis Fukuyo 1981

Figs 29a-h.

Previous descriptions: Fukuyo (1981): figs 30-34, 52, 53; Faust et al. (1996): figs 9-15; Hansen et al. (2001): pls 10C & D.

Taxonomic remarks: Ostreopsis lenticularis has a golden-brown chloroplast and a posterior nucleus (Fig. 29a). Cells are broadly oval in epithecal view (Figs 29a, b, d) and lentil-shaped in ventral view (Fig. 29e). The cell size ranges from 55 to 93 μm (77 ± 8.4 μm) dorsoventrally and 50 to 73 μm (63 ± 7.4 μm) in transdiameter (n = 25 cells). The thecal surface is smooth and perforated by numerous pores (Figs 29b - h). Two different sizes of valve pore are observed (Fig. 29h). The diameter of the larger pore, ranges from 0.2 to 0.4 μm and they are visible in the light microscope (Figs 29b, c). The diameter of the smaller pores ranges from 0.04 to 0.10 μm (Fig. 29h). Both types of pore have smooth edges, and they are evenly spaced on the valve surfaces (Fig. 29h).

The plate formula is Po, 3', 7", 6C, 6S?, Vp, Rp, 5'", 1p and 2'"" (Faust et al. 1996). The second apical plate (2') is small and narrow; it is the smallest plate in the epitheca (Fig. 29d). The first apical plate (1') is rectangular and positioned almost in the centre of the epitheca (Fig. 29d). The Po is curved, narrow, positioned off centre and on average 12 ± 0.7 μm long (n = 5) (Figs 29d, f). The 3' plate is more or less pentagonal and touches plates 1', 2', Po, 3", 4", 5" and 6" (Fig. 29d). Precingular plate 6" is the largest plate in the epitheca (Fig. 29d).

The cingulum is excavated and bordered by narrow lists (Figs 29d, e, g). The ventral plate (Vp) and the ventral pore (Vo) are located in the cingulum (Fig. 29g, arrow). The hypotheca consists of 8 plates viz. 5 postcingular plates, 1 posterior intercalary plate and 2 antapical plates (Fig. 29e). Plates 1'", 1"'' and 2'" are smaller than the other plates (Fig. 29e). Antapical plates 1'"" and 2'"" are very small and situated ventrally (Fig. 29e). Plate 1p is long, centrally located and touches plates 2'", 3'", 4'", 5'", 1'"" and 2'"" (Fig. 29e).

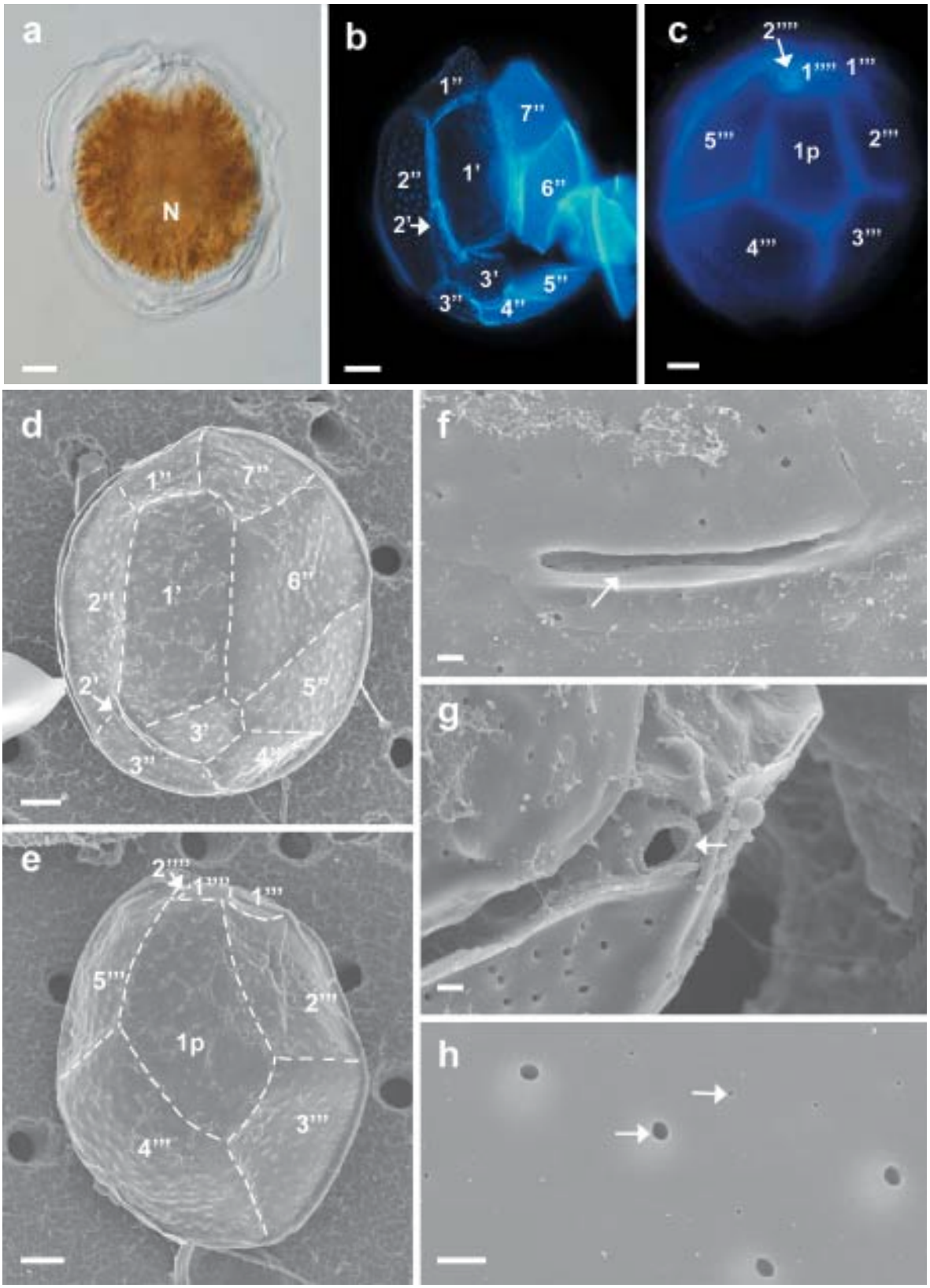
The morphological description of *O. lenticularis* from Malaysia fits with the original description of Fukuyo (1981). The Malaysian material differs from that described by Faust et al. (1996) in having a shorter apical pore plate (12 versus 16 μm long) and in the presence of two types of pores. This last feature was also reported by Fukuyo (1981) and Hansen et al. (2001).

Observations: This species was associated with *Sargassum* spp., *Padina* spp. and dead corals. It was observed in samples collected from Sipadan Island, Mabul Island, Tunku Abdul Rahman Park and Bak-Bak Beach.

Previous records: Ostreopsis lenticularis was first reported from Gambier Island in the Society Islands of French Polynesia, and New Caledonia by Fukuyo (1981). It was subsequently reported from the East China Sea and the Caribbean (Faust et al. 1996), Mascareignes Archipelago (Faust et al. 1996, Turquet et al. 1998, Hansen et al. 2001) and Indonesia (Sidabutar et al. 2000). It has been found in sand (Carlson & Tindall 1985, Faust et al. 1996), dead coral substrates (Carlson & Tindall 1985), algal turf in Réunion Island (Turquet et al. 1998, Hansen et al. 2001), plankton samples (Faust et al. 1996, Sidabutar et al. 2000) and associated with macroalgae (Faust et al. 1996). The biogeographic distribution reveals that this species is common in tropical areas.

Toxicology: A bioassay test showed *O. lenticularis* to be non-toxic to *A. franciscana*. However, the number of cells tested against *Artemia* larvae was low (200 cells/ml) due to difficulties in obtaining dense cultures. *Ostreopsis lenticularis* was previously found to produce a potent toxin that was toxic

Figs 29a-h. *Ostreopsis lenticularis*. 29a: Light micrograph (DIC) showing golden-brown chloroplast and a posterior nucleus (N); 29b, c: epifluorescence micrographs of epitheca and hypotheca, respectively; 29d-h: SEM; 29d, e: cells are broadly oval, and the thecal surface is smooth and perforated by numerous pores; 29d: epithecal view; plate 1' is rectangular and Po is positioned off centre; 29e: hypothecal view; 1p is long; 29f: Po is curved and narrow (arrow); 29g: the ventral plate containing the ventral pore (arrow) is situated in the ventral part of the cingulum; 29h: two different sizes of valve pores are present (arrows). – Scale bars in Figs 29a-e: 10 μm, Figs 29f-h: 1 μm.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to mice (Tindall et al. 1990) and two neuroactive compounds that were able to interact with nicotinic cholinergic receptors and voltage-dependent sodium channels (Mercado et al. 1995). The methanol extracts of the species were also found to influence the inward current in chick embryo neurons (Rivera-Rentas et al. 1995). Toxicity in *O. lenticularis* was suggested to be associated with a bacterium, *Pseudomonas* (González et al. 1995).

Ostreopsis ovata Fukuyo 1981

Figs 30a-i.

Previous descriptions: Fukuyo (1981): figs 35-38, 54, 55; Besada et al. (1982): figs 4-15; Faust et al. (1996): figs 16-23; Hansen et al. (2001): pl. 10, figs E & F.

Taxonomic remarks: Ostreopsis ovata contains a golden-brown chloroplast and a posterior nucleus (Fig. 30a). Cells are small, oval or tear-shaped in apical view (Figs 30a - e). The cell size ranges from 25 to 35 μm (32 ± 3.3 μm) dorsoventrally and 15 to 30 μm (23 ± 4.7 μm) in transdiameter (n = 30 cells). The thecal surface is smooth and perforated by pores (Figs 30d - i), which can be seen under the light microscope (Figs 30b, c). The pores have smooth edges (Fig. 30i). The pore diameter ranges from 0.13 to 0.28 μm.

The plate formula is Po, 3', 7", 6C, 6S?, Vp, Rp, 5'", 1p and 2'"" (Faust et al. 1996). The first apical plate (1') is long and situated almost in the middle of the epitheca (Fig. 30d). The 2' plate is small and narrow (Fig. 30d). The Po is straight to slightly curved, narrow and has an average length of 6.0 ± 0.8 μm (n = 5) (Figs 30b, d, f, g). It was considered to be associated with plate 2' by Faust et al. (1996). The 3' plate is medium-sized and triangular (Fig. 30d). Precingular plates 1", 3", 4", 5" and 7" are small compared to plate 2" and 6" (Fig. 30d).

The cingulum is excavated and bordered by lists (Figs 30d, e, f). The ventral plate (Vp) with the ventral pore (Vo) is situated in the cingulum (Fig 30h, arrow). The hypotheca consists of 8 plates (Fig. 30e). Postcingular plate 1'" is small and difficult to observe under the light microscope. Plates 2'", 3'", 4'" and 5'" are larger (Fig. 30e). Antapical plates 1'"" and 2'"" are very small and located ventrally (Fig. 30e). Plate 1p is long and medium-sized (Fig. 30e).

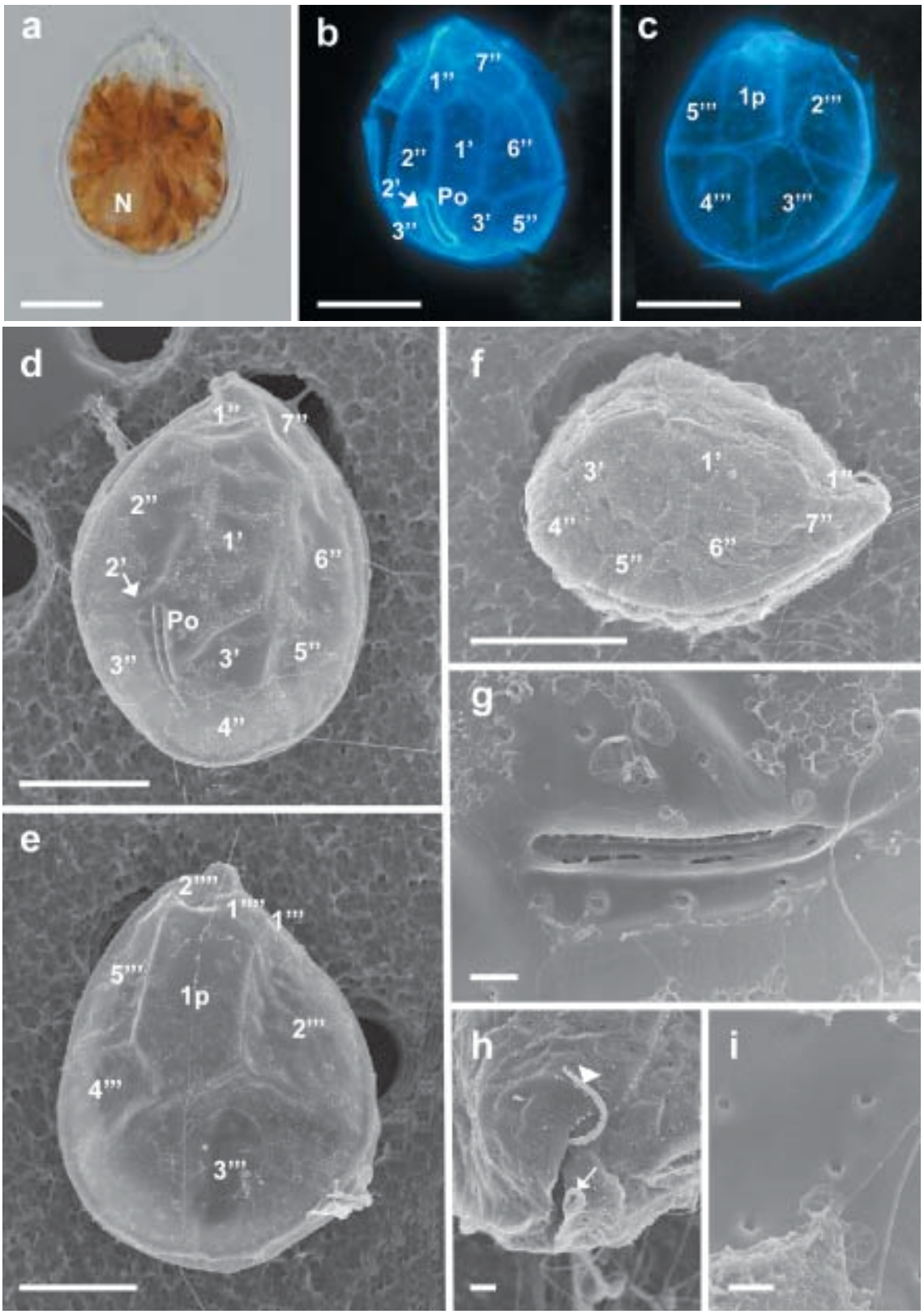
The morphological descriptions of *O. ovata* from Malaysia fits with the original description of Fukuyo (1981). However, the plate formula used by us follows the Kofoidean plate tabulation used by Norris et al. (1985) and Faust et al. (1996).

Observations: This is a common benthic species in Malaysian waters and it was observed from *Sargassum* spp., *Padina* spp., red algae, seagrasses and dead coral. It was found in samples collected from Tunku Abdul Rahman Park, Sepanggar Bay, Bak-Bak Beach, Mabul Island, Sipadan Island, Sandakan, Bangi Island, Pulau Tiga, Tanjung Datu, Tanjung Serabang and Port Dickson.

Previous records: Ostreopsis ovata was first discovered from French Polynesia, New Caledonia and Ryukyu Island by Fukuyo in 1981. It was present in samples collected from coral reefs. This species has also been reported from tide pools in the Caribbean Sea (Besada et al. 1982), water samples from the Tyrrhenian Sea (Tognetto et al. 1995), Indonesian waters (Sidabutar et al. 2000), Kenya (Hansen et al. 2001), the Caribbean Sea (Faust et al. 1996), on macroalgae from the East China Sea, Mascareignes Archipelago, the Carribbean Sea (Faust et al. 1996), Singapore (Holmes et al. 1998) and Malaysia (Port Dickson, Pulau Redang, Kota Kinabalu) (Leaw et al. 2001), in submerged sand of the East China Sea, Mascareignes Archipelago and the Carribbean Sea (Faust et al. 1996) and Singapore (Holmes et al. 1998) and in algal turf samples from Réunion and Zanzibar (Hansen et al. 2001). These recordings reveal it to be a subtropical and tropical species that occurs in plankton, as epiphyte and in benthic environments (Faust et al. 1996).

Toxicology: Bioassay tests of 20 strains of *O. ovata* revealed that 16 strains were non-toxic to *A. franciscana* while 4 strains were toxic. *Ostreopsis ovata* has been reported to produce a butanol-soluble compound which is lethal to mice (Nakajima

Figs 30a-i. *Ostreopsis ovata*. 30a: Light micrograph (DIC) of live cell showing golden-brown chloroplast and nucleus (N); 30b, c: epifluorescence micrographs of epitheca and hypotheca, respectively; 30d-i: SEM; 30d, e: cells are oval or tear-shaped, the thecal surface is smooth and perforated by pores; 30d: epithecal view; plate 1' is long and Po is situated off centre; 30e: hypothecal view; plate 1p is long and medium-sized; 30f: the cell is anterior-posteriorly compressed; 30g: Po is straight to slightly curved and narrow; 30h: ventral view, the ventral pore (arrow) is situated in the ventral plate, and the longitudinal flagellum emerges from the sulcus (arrowhead); 30i: valve pores with smooth edges. – Scale bars in Figs 30a-f: 10 μm, Figs 30g-i: 1 μm.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et al. 1981). Methanol extracts from cultures of *O. ovata* were not toxic to mice (Tindall et al. 1990).

Order Gymnodiniales Apstein 1909

Fensome et al. (1993) classified species in the Gymnodiniales on the basis of the arrangement of the amphiesmal vesicles, which may or may not contain plates. The amphiesmal vesicles usually are arranged randomly and may be present in thousands to a few hundred per cell. The cell is uninucleate or multinucleate, may or may not possess specialized internal structures or organelles and plastids. Generally the cells are free-living, but some species may possess a peduncle adapted to parasitism. The order consists of 5 families: Gymnodiniaceae, Polykrikaceae, Warnowiaceae, Actiniscaceae and Dicroerismaceae.

In this order, two species from the genus *Amphidinium* (viz. *A. carterae* and *A. operculatum*) were identified. Recently, based on the partial sequence data of LSU rDNA, the placement of the genus *Amphidinium* in this order was questioned (Daugbjerg et al. 2000, Fløe-Jørgensen et al. 2004) and the genus was redefined to comprise cells with a minute irregular triangular or crescent-shaped epicone. Cells are dorsoventrally flattened, with or without chloroplasts (Flø Jørgensen et al. 2004).

Amphidinium carterae Hulburt 1957

Figs 31a-c.

Synonym: Amphidinium microcephalum Norris 1961

Previous descriptions: Murray et al. (2004a): figs 2F, 3E, 8, A-F.

Taxonomic remarks: The nucleus is located posteriorly and a pyrenoid is present centrally (Fig. 31b). The chloroplast is situated around the cell periphery, some radiating from the pyrenoid (Fig. 31b). Cells are oblong to oval in ventral view (Fig. 31c) and dorso-ventrally compressed (Fig. 31a). The cell in Fig. 31b has rounded off due to extended observation in the microscope. In ventral view the epicone is deflected to the left and it is minute compared to the hypotheca (Figs 31b-c). The cell size ranges from 15 to 24 μm (19 ± 1.9 μm) in length and from 13 to 23 μm (17 ± 2.0 μm) in width (n = 30 cells). The thecal surface is smooth (Figs 31c). A pore of the longitudinal flagellum and a ventral ridge is present on the hypocone (Fig. 31c). The flagellar pore is located almost at the centre of the hypotheca (Fig. 31c).

Observations: Amphidinium carterae was observed from *Sargassum* sp. in Port Dickson, Peninsular Malaysia.

Previous records: Murray et al. (2004a) considered *A. carterae* a cosmopolitan species, which inhabits both marine sediments and the water column. It is also known as a symbiont of the jellyfish *Cassiopeia xamachana*. Phylogenetic studies showed that *A. carterae* can be divided into at least 2 genotypes. However, the distribution pattern of these two genotypes showed no relation biogeographically but indicated a cosmopolitan distribution of the species (Murray et al. 2004a).

Toxicology: Bioassay test showed that *A. carterae* was not toxic to *A. franciscana*.

Amphidinium operculatum Claparède et Lachmann 1859

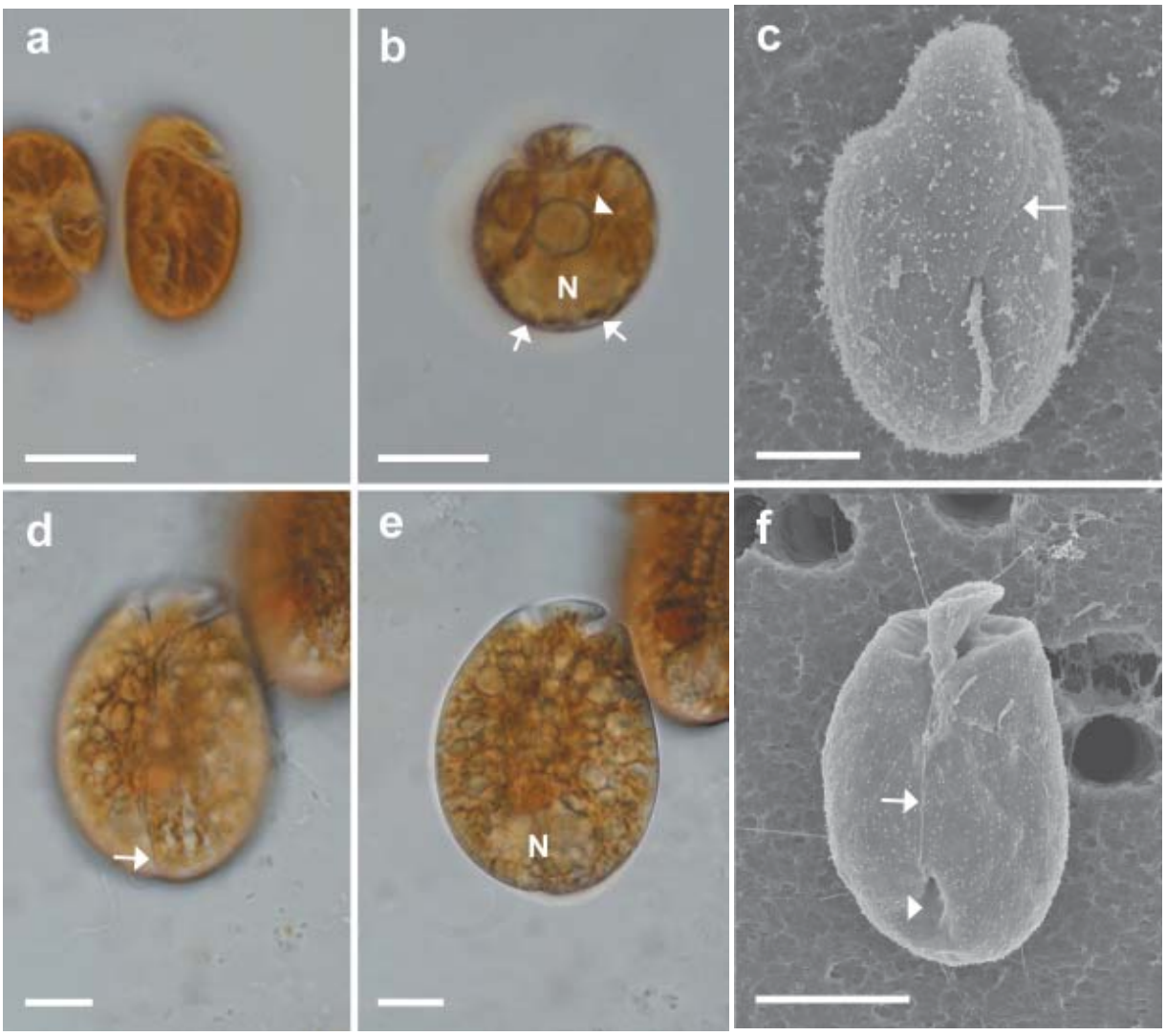
Figs 31d-f.

Synonym: Amphidinium elegans Grell et Wohlfarth-Bottermann 1957

Previous descriptions: Murray et al. (2004a): figs 1, A-F, 2A, 3A.

Taxonomic remarks: Cells with nucleus located posteriorly and numerous round orange to yellow globules in the cells (Figs 31d, e). Cells are oval in ventral view (Figs 31d, f) and dorso-ventrally compressed. The epitheca is small, triangular and deflected to the left (Figs 31d - f). The hypotheca is large (Figs 31d - f). The cell size ranges from 33 to 53 μm (44 ± 5.7 μm) in length and 23 to 38 μm (31 ± μm) in width (n = 25 cells) for specimens collected in Pulau Tiga and from 28 to 38 μm (33 ± 3.6 μm) in length and 23 to 30 μm (25 ± 2.9 μm) in width for specimens observed in Sepanggar Bay. The surface is smooth (Fig. 31f). The posterior part of the hypotheca is broadly oval (Figs 31d - f). The hypotheca comprises a flagellar pore in the cell posterior (Fig. 31f). A narrow and long ventral ridge is situated between the epitheca and the flagellar pore (Fig. 31f).

Observations: Amphidinium operculatum was found in samples collected from Tunku Abdul Rahman Park, Bak-Bak Beach, Pulau Tiga, Sepanggar Bay and Tanjung Datu, associated with *Sargassum* spp., *Padina* spp. and dead corals.



Figs 31 a-c. *Amphidinium carterae*. 31a-b: Light micrographs (DIC); 31a: the cell is dorso-ventrally compressed; 31b: cell with central pyrenoid (arrowhead), a posterior nucleus (N) and chloroplast is positioned at the cell periphery (arrows); 31c: SEM; ventral view showing ventral ridge (arrow) and flagellar pore situated almost at the centre of the hypotheca. – Figs 31d-f. *Amphidinium operculatum*. 31d-e: light micrographs (DIC); 31d: ventral view showing the longitudinal flagellum emerging from the ventral pore (arrow); 31e: cell showing posterior nucleus (N); 31f: SEM; the cell is dorso-ventrally compressed; a narrow and long ventral ridge (arrow) is present and a flagellar pore is visible at the cell posterior (arrowhead). – Scale bars in Figs 31a-f: 10 μm.

Previous records: The characteristics of this species have recently been revised by Flø Jørgensen et al. (2004) and Murray et al. (2004a).

Toxicology: Bioassay tests revealed that *A. operculatum* was not toxic to *A. franciscana*.

Order Peridiniales Haeckel 1894

In the Peridiniales, plate tabulation is one of the most important features for species identification. Each genus is circumscribed by a specific tabulation formula. Thus in 1998, Faust & Steidinger proposed a new genus, *Bysmatrum* for three benthic scrippsielloid species which agreed in thecal tabulation

and apex morphology (B. *subsalsum* (Ostenfeld) Faust & Steidinger, *B. arenicola* (Horiguchi et Pienaar) Faust & Steidinger and B. *caponii* (Horiguchi & Pienaar) Faust et Steidinger. Later, in 2001, Ten-Hage et al. described *B. granulosum* from St Leu, Réunion Island. The specific characters for the genus are as follows: the apical plate 1' is wide, asymmetric and pentagonal and reaches the anterior margin of the cingulum; intercalary plates 2a and 3a are separated by apical plate 3' and precingular plate 4"; the apical pore complex is a recessed chamber with a large Po plate, an elongated X plate, and a raised dome at the centre; six cingular plates and four sulcal plates are present; the thecal surface is vermiculate to reticulate (Faust & Steidinger 1998). In this study, two *Bysmatrum* species were identified.

One species of *Peridinium* from the subfamily Peridinioideae was identified in the samples. Species of the genus *Peridinium* are characterized by a cingulum of 4 to 6 cingular plates exclusive of the transitional plate, where present, and with at least one intercingular boundary on the dorsal side (Fensome et al. 1993).

Bysmatrum caponii (Horiguchi et Pienaar) Faust et Steidinger 1998

Figs 32a-k.

Basionym: Scrippsiella caponii Horiguchi et Pienaar 1988, p. 38, figs 3-12, 15-17.

Synonym: Peridinium gregarium Lombard et Capon 1971

Previous description: Horiguchi & Pienaar (1988): figs 3-12.

Taxonomic remarks: Cells are pentagonal in ventral and dorsal view (Figs 32a, i, j). The cell length ranges from 18 to 24 μm (22 ± 2.8 μm) and the width from 19 to 26 μm (23 ± 2.7 μm) (n = 5 cells). The thecal surface is reticulated (Figs 32g - k) with scattered pores (Fig. 32k). Many pores are located at the periphery of the thecal plates (Fig. 32k).

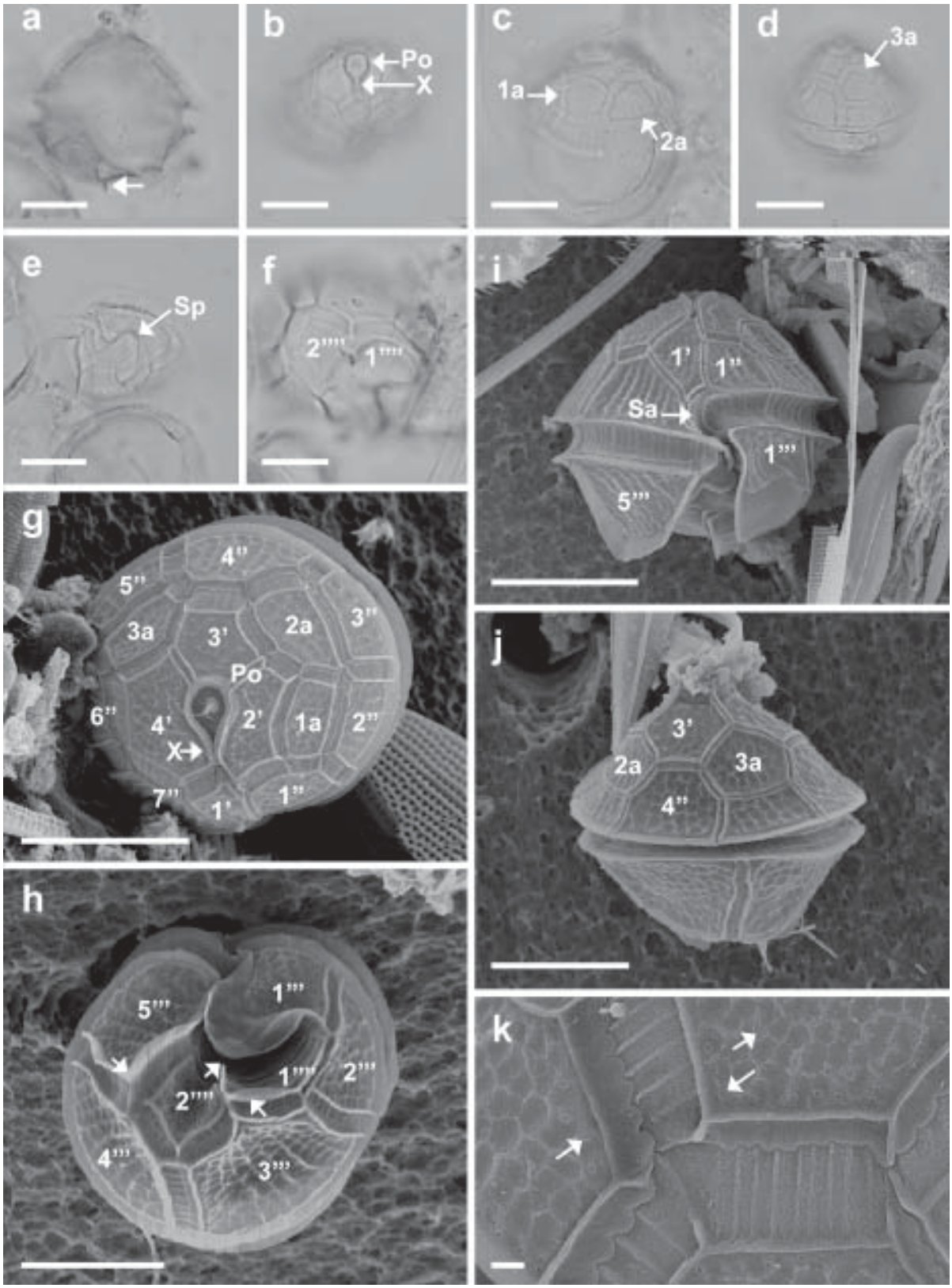
Thecal tabulation is Po, X, 4', 3a, 7", 6c, 5'", 2'"" and 4s (Horiguchi & Pienaar 1988). All thecal plates are separated by striated intercalary bands (Figs 32g - k). In older cells, the rims of the thecal plates grow into a ridge with a wave-like border (Fig. 32k). The apical pore complex (Po) is polygonal and touches the plates X, 2', 3' and 4' (Figs 32b, g). Inside the Po, the round apical dome contains an apical stalk (Fig. 32g, centre). The stalk produces mucus strands that anchor the cells to the substrate (Lombard & Capon 1971a, Horiguchi & Pienaar 1988, Faust & Steidinger 1998). The canal plate (X) is narrow and elongate and connects the apical pore plate with the 1' plate (Figs 32b, g). The first intercalary plate (1a) is 4-sided (Figs 32c, g), 2a is 6-sided (Figs 32c, g) and 3a is 5-sided (Figs 32d, g, j). The side between plate 2a and 2" is counted as one of the sides in determining the total sides in 2a (Figs 32c, g). The second intercalary plate (2a) is separated from 3a by plates 3' and 4" (Figs 32g, j). The first apical plate (1') is 5-sided (Fig. 32i) and touches the Sa and the canal plate (Figs 32g, i).

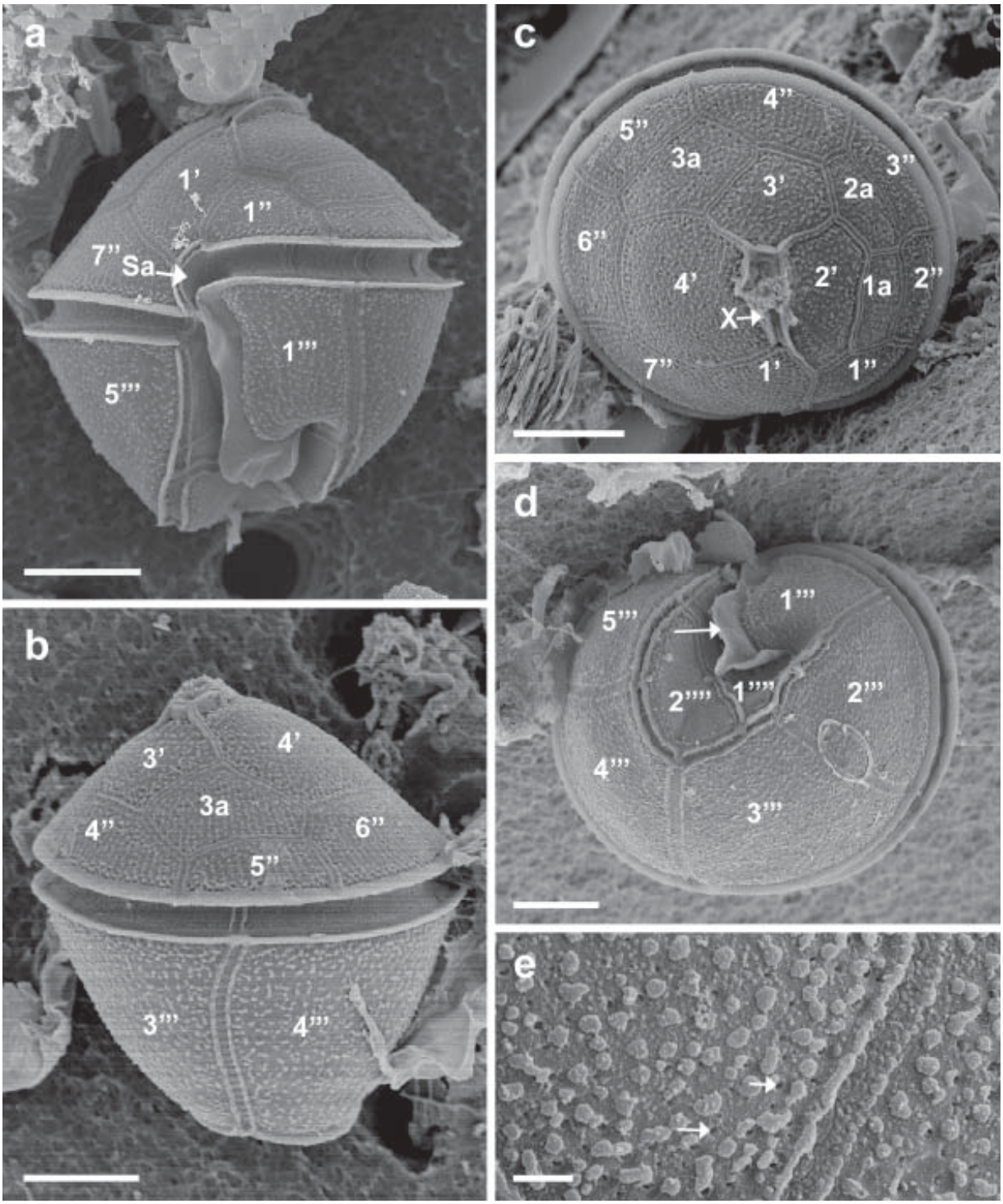
The cingulum is deep and transversely striated (Fig. 32i). The sulcus is narrow, deeply excavated and consists of 4 plates. The anterior sulcal plate (Sa) borders plate 1', 1", 7" and the cingulum (32i). The posterior sulcal plate (Sp) is larger than the other sulcal plates and does not touch the cingulum (Figs 32e, i). The postcingular plates 1'" and 5'" have distinct lists (Figs 32h, i) which appear as spines under the light microscope (Fig. 32a). The first antapical plate (1'"") is small, narrow and also ornamented with a prominent list (Figs 32f, h). In some cells it is hardly visible (Fig. 32h). Horiguchi and Pienaar (1988) observed spines on the left side of the posterior end of the cell and on plate 1'"" near the suture between the plates 1'"" and 2'"". Such spines were not seen in our material.

Observations: Bysmatrum caponii was observed in preserved samples from Tunku Abdul Rahman Park, Bak-Bak Beach, Sipadan Island and Mabul Island. It was associated with *Sargassum* spp., *Padina* spp. and seagrasses.

Previous records: Bysmatrum caponii was first described as *Peridinium gregarium* by Lombard and Capon (1971b). It was found in small rock tide pools

Figs 32a-k. *Bysmatrum caponii*. 32a-f: Light micrographs (DIC); 32a: the list on the postcingular plates appears as spines (arrow); 32b: epithecal view with polygonal Po and narrow canal plate (X); 32c: dorsal view with 4-sided 1a and 6-sided 2a; 32d: 3a is 5-sided; 32e: hypotheca with posterior sulcal plate (Sp); 32f: antapical plates 1'"" and 2'""; 32g-k: SEM; 32g: epithecal view showing plate tabulation; 32h: hypothecal view with distinct lists on 1'", 5'" and 1'"" (arrows); 32i, j: cells are pentagonal, and the thecal surface is reticulated; 32j: 2a and 3a are separated by 3' and 4"; 32k: pores occur scattered on the thecal surface, but are more numerous near the periphery of the plates (arrows). – Scale bars in Figs 32a-j: 10 μm, Fig. 32k: 1 μm.


a
b
Po
X
c
1a
2a
d
3a
e
Sp
f
2''''
1''''
i
1'
1''
Sa
1'''
5'''
g
4''
5''
3a
3'
2a
3''
Po
6''
4'
2'
1a
2''
X
7''
1'
1''
j
3'
2a
3a
4''
h
5'''
1'''
1''''
2'''
2''''
4'''
3'''
k



Figs 33a-e. *Bysmatrum granulosum*. 33a-e. SEM; 33a, b: cells are oblong to pentagonal and the thecal surface is ornamented with wart-like projections; 33a: ventral view; the sulcus is narrow, deeply excavated and the left side is ornamented with a distinct list; 33b: dorsal view; 3a is 5-sided; 33c: epithecal view; the canal plate (X) is narrow, elongated and connects the apical pore plate with 1'; 2a and 3a are separated by 3' and 4''; 33d: hypothecal view showing left sulcal list protruding posteriorly (arrow); 33e: small pores in the thecal surface (arrows). – Scale bars in Figs 33a-d: 10 μm, Fig. 33e: 1 μm.

on the coast of Southern California and occurred in large numbers to form cloud-like masses held together by a mucous matrix (Lombard & Capon 1971a). In 1979b, Loeblich III et al., examined culture UTEX 1948 which was isolated from the same tide pool. Loeblich III et al. (1979b) considered this culture to be identical to *Peridinium gregarium* Lombard et Capon which they transferred to *Scrippsiella* as *Scrippsiella gregaria*. However, in 1988, Horiguchi and Pienaar re-examined the type material of *P. gregarium* Lombard et Capon after finding *P. gregarium*-like cells in a tide pool in Cape Sunosaki, Japan and they discovered that *P. gregarium* was not identical to UTEX 1948. Based on thecal arrangement, *P. gregarium* was transferred to *Scrippsiella* as *Scrippsiella caponii* and Loeblich III et al.'s (1979b) combination *S. gregaria* being invalid.

Toxicology: Unknown.

Bysmatrum granulosum Ten-Hage, Quod, Turquet et Couté 2001

Figs 33a-e.

Previous descriptions: Ten-Hage et al. (2001): figs 9-27.

Taxonomic remarks: Cells are oblong to pentagonal in ventral and dorsal view (Figs 33a, b). The cell is subcircular in epithecal and hypothecal view (Figs 33c, d). Its length ranges from 34 to 46 μm (40 ± 4.2 μm) and the width from 28 to 38 μm (37 ± 6.1 μm) (n = 5 cells). The thecal surface is ornamented with wart-like projections and scattered small pores (Figs 33a - e).

Thecal tabulation is Po, X, 4', 3a, 7", 6c, 5'", 2'"" and 4s (Ten-Hage et al. 2001). All thecal plates are clearly separated from each other by distinct intercalary bands (Figs 33a - d). The apical pore complex (Po) is polygonal and touches X, 2', 3' and 4' (Figs 33c). The canal plate (X) is narrow, elongated and connected to the apical pore plate and 1' (Fig. 33c). The first intercalary plate (1a) is 4-sided (Fig. 33c), 2a is 6-sided (Fig. 33c) and 3a is 5-sided (Figs 33b, c). The side between plate 2a and 2" is counted as one when determining the total of sides on plate 2a (Fig. 33c). The second intercalary plate (2a) is separated from 3a by plates 3' and 4" (Figs 33b, c). The first apical plate (1') is 5-sided and touches Sa and the canal plate (Fig. 33a).

The cingulum is deep and consists of 6 plates (not shown). The sulcus is narrow, deeply excavated and ornamented on the left side with a distinct list that protrudes posteriorly (Figs 33a, d). The anterior sulcal plate (Sa) border plates 1', 1", 7" and the cingulum plates (Fig. 33a). The posterior sulcal plate (Sp) is larger than the other sulcal plates and does not touch the cingulum (not shown). The hypotheca has five postcingular plates and two antapical plates (Fig. 33d). The antapical plate 1'"" is small and 4-sided (Fig. 33d). The second antapical plate (2'"") is 5-sided (Fig. 33d).

Observations: Bysmatrum granulosum was observed in preserved samples from *Sargassum* spp., *Padina* spp. and seagrass on Sipadan Island, east of Sabah.

Previous records: Bysmatrum granulosum was first identified from sediment and coral samples collected from Réunion Island, South West Indian Ocean (Ten-Hage et al. 2001)

Toxicology: Unknown.

Peridinium quinquecorne Abé 1927

Figs 34a-c.

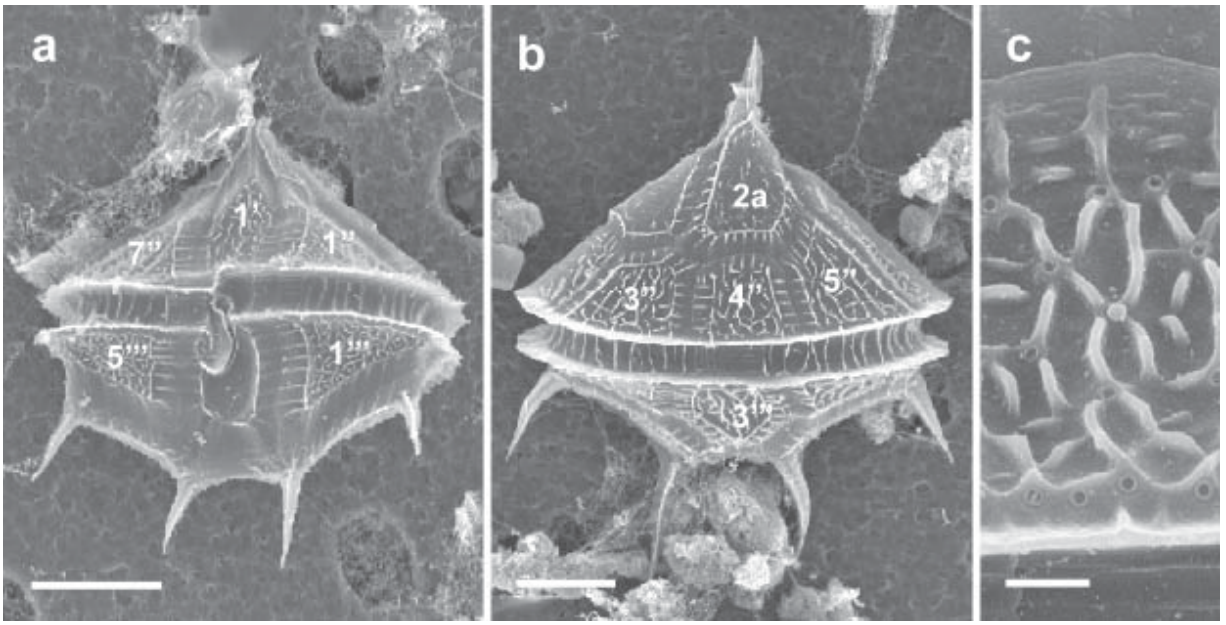
Previous descriptions: Abé (1981): figs 264-272; Horiguchi & Pienaar (1991): figs 1-24; Murray (2003): figs 2.19a-g.

Taxonomic remarks: The cell is *c*. 40 μm long and *c*. 32 μm wide. The thecal surface is reticulated (Figs 34a-c). Pores are distributed on the valve surface (Fig. 34c). The plate formula is PP, X, 3', 2a, 7", 5c, 4s, 5'", 2'"" (Horiguchi and Pienaar 1991). The first apical plate (1') is ortho (Fig. 34a). The cingulum is excavated, vertically striated and surrounded by lists (Figs 34a, b). The sulcal area is oblong and situated in a shallow depression (Fig. 34a). Four long and pointed spines protrude posteriorly and one points anteriorly (Figs 34a, b).

Observations: This species was observed in samples preserved from *Sargassum* spp, *Padina* spp and seagrasses in Bak-Bak Beach, north of Sabah.

Previous records: This species was found in Asamushi, Japan (Abé 1981), in tide pools in South Africa (Horiguchi and Pienaar 1991), in the Philippines (Horiguchi & Sotto 1994) and in Australia (Murray 2003). Cells were reported to vary in shape and length of the antapical spines (Horiguchi and Pienaar 1991).

Toxicology: Unknown.



Figs 34a-c. SEM of *Peridinium quinquecorne*. 34a, b: ventral and dorsal view respectively, showing four long, pointed antapical spines; 34c: the thecal surface is reticulated. – Scale bars in Figs 36a-b: 10 μm, Fig. 34c: 1 μm.

Incertae sedis

Pileidinium ciceropse Tamura et Horiguchi

Figs 35a-f.

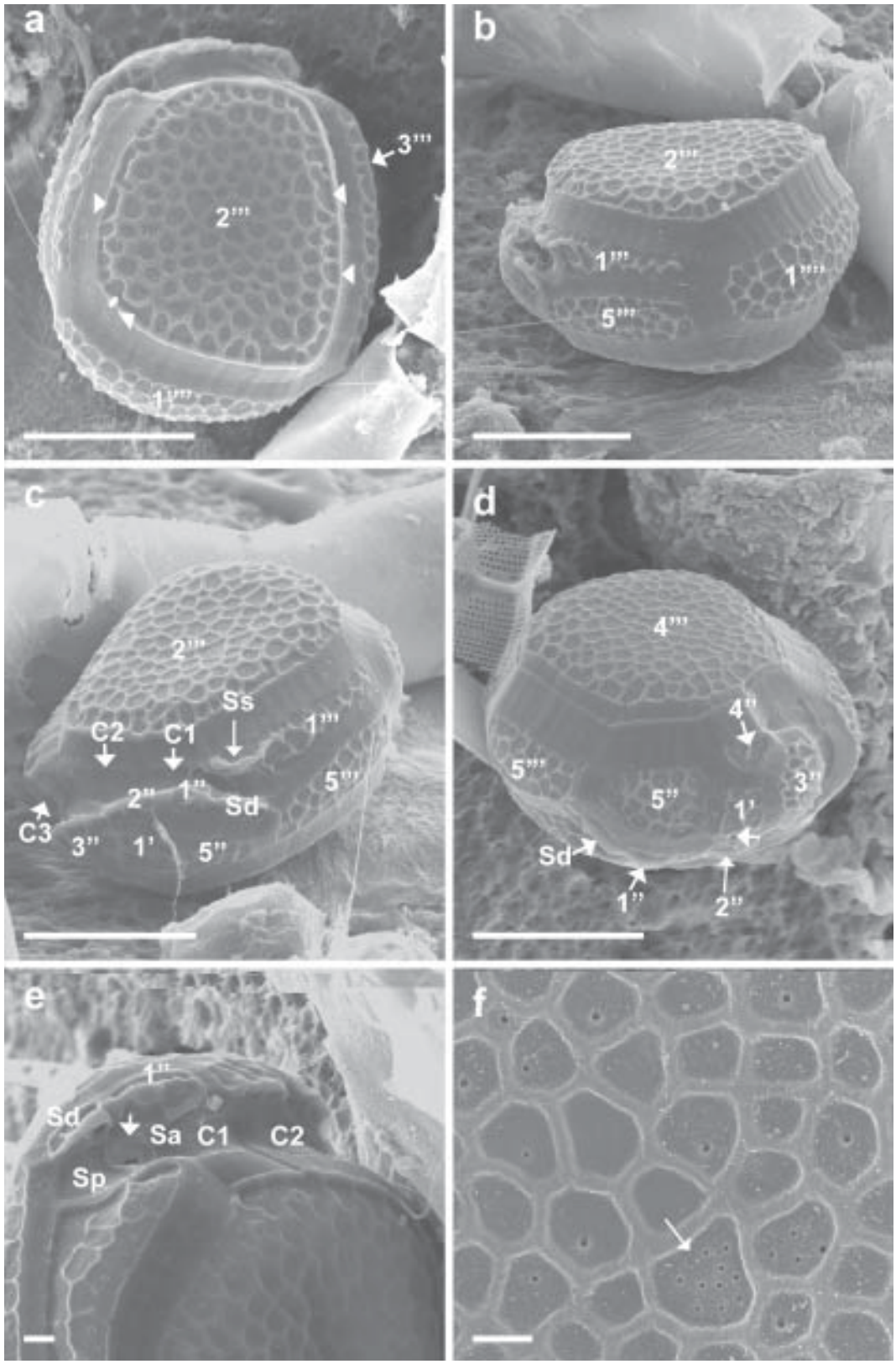
Previous description: Tamura & Horiguchi (2005): figs 1-15, figs 28-32.

Taxonomic remarks: Cells from Sabah are rectangular in left lateral view (Fig 35a). The cell size is c. 23 μm long and 23 μm wide. Thecal plates are thick and markedly reticulated (Figs 35a - f). Many of the polygonal shallow depressions are perforated by pores of various sizes (Fig. 35f). Some depressions lack perforations (Fig. 35f). Depressions with many pores are mostly situated near the plate periphery (Figs 35a - c).

The epitheca is small compared to the hypotheca and cap-shaped (Figs 35c - e). The plate formula is 1', 5'', 4c, 4s, 5''', 1'''' (Tamura & Horiguchi 2005). Plate 1' is rectangular and touches plate 2'', 3'', 4'' and 5'' (Figs 35c, d). A pore is situated between plate 1' and 2''. Plate 1'' is narrow. Plate 3'' is wedge-shaped and borders plates 1', 2'' and 4'' (Fig. 35d). Plate 4'' is small, triangular and 4-sided (Fig. 35d). Plate 5'' is the largest plate on the epicone and touches plate 1', 1'', 2'', 4'', 4''', 5''' and the right sulcal plate (Sd) (Figs 35c, d).

The cingulum is incomplete and made of 4 rectangular plates (Figs 35a, c, e). The sulcus consists of an anterior sulcal plate (Sa), a posterior sulcal plate (Sp), a left sulcal plate (Ss) and a right sulcal plate (Sd) (Figs 35c - e). The pore is probably the flagellar pore (Fig. 35e). The hypotheca consists of six plates. Plates 2''' and 4''' are oval to rectangular and the largest plates on the hypocone (Figs 35a, c, d). Plates 1''' and 5''' are long and narrow (Figs 35b, c). Plate 1''' tapers posteriorly

Figs 35a-f. *Pileidinium ciceropse*. 35a-f: SEM; 35a: left lateral view, the thecal surface is thick and reticulated. Depressions with numerous pores are mostly situated near the plate periphery (arrowheads); 35b: oblique ventral view; the cell is compressed. Plates 1''' and 5''' are long and narrow; 35c, d: oblique apical views showing incomplete cingulum; 35c: a small left sulcal plate (Ss) is present on the left side of the sulcus (arrow); 35d: plate 4'' is small and triangular and a pore is present between plate 1' and 2'' (arrow); 35e: sulcal area with anterior sulcal plate (Sa), posterior sulcal plate (Sp) and a pore plate with a pore (arrow); 35f: polygonal shallow depression on the thecal surface with one or more pores (arrow); some depressions lack pores. Scale bars in Figures 35a-d: 10 μm, Figures 35e, f: 1 μm. Abbreviations: C1-C3, cingular plate; Sa, Sd, Ss, Sp, sulcal plate.


a
3'''
2'''
1''''
b
2'''
1'''
1''''
5'''
c
2'''
Ss
C2
C1
1'''
5'''
2''
1''
Sd
C3
3''
1'
5''
d
4'''
4''
5'''
5''
3''
1'
Sd
1''
2''
e
1''
Sd
Sa
C1
C2
Sp
f

(Figs 35b, c). Plate 5''' is rectangular (Figs 35b, c). Plate 1'''' is rectangular (Fig. 35b) and appears convex in left lateral view (Fig. 35a).

Observations: Pileidinium ciceropse was observed in samples preserved from seagrasses in Sipadan Island.

Previous record: This species has a yellow-brown chloroplast and was described recently from a sandy beach on Mecherchar Island, Republic of Palau (Tamura & Horiguchi 2005).

Discussion

A total of 9 genera and 24 species were identified in the studied areas in Malaysia (Table 11). The list includes eight species known to produce phycotoxins. In Singapore, in a survey of marine benthic dinoflagellates from coral reefs, a lower number of benthic species was found: 7 genera of dinoflagellates were identified from macroalgae, turf algae and coral rubble (Holmes et al. 1998). Murray (2003), however, reported 56 sand-dwelling dinoflagellates from Southern Australia belonging to Gymnodiniales, Gonyaulacales, Peridiniales, Phytodiniales and Prorocentrales and in a study of marine benthic dinoflagellates from the SW Indian Ocean, Turquet et al. (1998) identified 39 species from 12 genera at coral reefs. The high or low number of species recorded undoubtedly reflects the sampling strategies used (collection method, seasonal distribution of species, substrates examined, location of sampling sites and sampling duration).

That the sampling strategies is important was illustrated by Hoppenrath & Elbrächter (1998) who searched for sand-dwelling *Roscoffia capitata* using different methods of collection, but succeded only after applying the extraction method of Uhlig (1964). Hansen et al. (2001) suggested that the difference in number of ciguatera-producing dinoflagellates found in Réunion and in Mauritius may be due to the different substrates sampled, macroalgae in Mauritius and dead coral with algal turf in Réunion. In Belize, high cell numbers of epiphytic dinoflagellates were found on brown algae and red algae, but lower numbers on green algae and angiosperms (Morton & Faust 1997). The population density of the dinoflagellates differed between the species of macroalgae and even among individuals of the same population (Nakahara et al. 1996). The differences may due to growth factors provided by the macroalgae and other organisms in the substrates (Morton & Faust 1997, Nakahara et al. 1996). Tindal & Morton (1998) showed that the community structure of epibenthic dinoflagellates depends on the type of ecosystems. Thus, the reef has a low species diversity compared to mangrove-fringed coves.

In tropical countries, annual monsoons may be one of the factors that affect the abundance of marine benthic species. Malaysia faces the southwest monsoon in the dry season from April to October and northeast monsoon in the wet season from October to February. These monsoons have been reported to be responsible for the *Pyrodinium* blooms, particularly in Sabah (Usup et al. 1989). In Indonesia, high densities of toxic phytoplankton were recorded during the wet season due to nutrient enrichments (Sidabutar et al. 2000). In this study, samples were collected twice, one time at the end of the dry season and the other at the end of the wet season. The diversity of species was not significantly different however, but more frequent sampling may give a different result. According to Lüning (1990), the monsoon causes seasonal periodicities in the seaweed flora. During the dry season, most of the macroalgae disappear. During the wet season, the macroalgae resume growth and form new thallus branches, while old thallus parts are torn off by the heavy wave action. Numerous species become fertile during the wet season. The seasonal periodicity of macroalgae, combined with the changing of chemical and physical factors in the sea, may reduce or increase the density of benthic organisms at any particular sampling period. In temperate areas, the cell densities of benthic dinoflagellates is reported to vary seasonally, highest cell densities occurring during the winter to summer transition period (Turquet et al. 1998).

The dinoflagellates collected during the present study were commonly associated with *Sargassum* spp. and *Padina* spp. (Table 11). These species are often the dominant macroalgae in Sabah (De Silva et al. 1999) and they also serve as substrate in other parts of the world (Tindall & Morton 1998). The high abundance of benthic dinoflagellates on brown algae has been suggested to be due to a nutritional link between the dinoflagellates and the macroalgae (Heil et al. 1998). In all study sites in Malaysia, the most common benthic species were *Prorocentrum lima* and *Ostreopsis ovata*. *Prorocentrum lima* was observed on all types of substrates in the sampling areas, but *O. ovata* preferred substrates with high surface area such as the macroalgae and the seagrasses, to which they attach by mucus threads. *Prorocentrum lima* has also been reported as a dominant species in southern Australia (Murray 2003) and in Belize (Morton & Faust 1997) whereas *O. ovata was* reported as a dominant species in Sin-

gapore reefs (Holmes et al. 1998). In this study, Sipadan Island had the highest species diversity among the sites examined (Table 11). Sipadan Island is a pristine island, situated in the Celebes Sea and hosts only tourist resorts. The high diversity of benthic species is frequently observed at undisturbed islands with coral reefs and very few inhabitants (e.g. Faust 1997).

Among the 24 species of dinoflagellates identified from Malaysia, fourteen were established into culture. They were tested for toxicity to the brine shrimp, *Artemia franciscana*. Six species (viz. *Prorocentrum arenarium, P. lima, Gambierdiscus pacificus, Ostreopsis labens, O. ovata* and *Coolia tropicalis*) were toxic to *A. franciscana,* and two other species (viz. *P. concavum* and *P.* cf. *faustiae*) caused immediate inactivation of movement of the *Artemia* larvae when the two organisms were mixed. The immobility of *Artemia* larvae may be due to a neurotoxin that inhibits movement of limbs and antenna but does not kill the larvae. Bioassay tests using *Artemia* spp. have been applied in aquatic toxicology for more than 20 years (Prokic et al. 1998) and for dinoflagellates, this method has been used to test toxicity of *P. lima, A. tamarense* and *A. carterae* (Demaret et al. 1995, Prokic et al. 1998, Ismael et al. 1999). It has been recommended as a useful tool for screening of dinoflagellate toxicity (Quod et al. 1995).

We have also examined the toxicity of several strains of the same species. The results showed that not all strains of species known as toxin producers are toxic. Thus, 16 of 20 strains of *Ostreopsis ovata* were non-toxic to *A. franciscana*. Six strains of *Coolia* sp. were toxic and one strain was non-toxic. The difference in toxicity of isolates from different localities has long been recognized (e.g. Morton & Tindall 1995) and toxin production may be influenced by growth phase and abiotic factors such as temperature, salinity, pH, light, nitrogen and phosphorus (Steidinger 1993).

The findings of the potentially toxic benthic species in the sampling areas suggested that Malaysia can expect more HAB problems in the future. Previous studies have shown that benthic species may be responsible for diarrhetic shellfish poisoning (DSP), ciguatera fish poisoning (e.g. Murakami et al. 1982, Holmes et al. 1991) and palytoxin (Lenoir et al. 2004). Two benthic species (*G. toxicus* and *P. lima*) have therefore, in several countries, been added to the list of HAB species monitored in fish and shellfish industries (Anderson et al. 2001). For example, in Hawai where ciguatera fish poisoning occurs regularly, the Department of Health (DOH) maintains a database to track the occurrence of ciguatera cases. The fishermen are provided with free test kits from the Hawaiian Government to test the fish for ciguatoxin, thus helping to protect public health. In Norway, Denmark and New Zealand, *P. lima* is one of the species monitored in fish and shellfish industries. Testing of shellfish flesh for toxicity is conducted when the cell concentration of *P. lima* is 500 cellsL^{-1} or more.

Order Prorocentrales

A total of 11 species of *Prorocentrum* were identified in this study using the characteristics suggested by Faust (1993a, 1993b, 1994) and others (Morton 1998, Ten-Hage et al. 2000a). However, in order to apply these morphological features, cells must be observed under the scanning electron microscope, which can be time consuming especially for species that produce large amounts of mucus covering the critical details in the SEM. Epifluorescence microscopy is a useful alternative for routine monitoring of species of *Prorocentrum.*

Most *Prorocentrum* species identified generally fit with previous descriptions except for differences in size and shape of the cells. Faust (1991) found that *P. lima* collected from many geographic areas showed varied in shape. Hence, it was concluded that these characters should be given less importance in species identification. Other characters found to differ from previous taxonomic decriptions are the number of valve pores and marginal pores and the number of platelets in the periflagellar area. Both features are difficult to determine even in SEM and therefore of less importance for routine species identification. Useful features in species determination of the genus *Prorocentrum*, are size and shape of the cell, the ornamentation of the periflagellar area (presence or absence of flange or spine) and valve surface (the arrangement and the different sizes of the pores and the presence or absence of marginal pores) and the presence of pyrenoid.

The periflagellar area of *P. emarginatum* is thought to consist of 5-6 platelets. Unfortunately the number of platelets was not discussed in previous studies (e.g. Fukuyo 1981, Faust et al. 1999 and Faust 1990). In *P.* cf. *faustiae*, only one morphological characteristic does not fit with the original description i.e. number of platelets at the periflagellar area where we observed 8-9 platelets, while Morton (1998) reported 16 platelets. Another species that is closely resembled *P. faustiae* is *P. arabianum* described from Gulf of Oman (Morton et al. 2002). According to Morton et al. (2002), *P. arabianum* is distinguished by having asymmetrical cell shape in

Table 11. List of benthic marine dinoflagellates identified from Sabah (TAR=Tunku Abdul Rahman Park, SB=Sepanggar Bay, Island) and Malaysian Peninsula (PD=Port Dickson) according to substrates collected (S=*Sargassum* spp., P=*Padina* spp., DC= site. SD=sampling date. * Pelagic species.

Locations	Sabah SD: 20, 25, 28/08/03 (TAR); 22/08/03 (SB); 9/09/03 (BB); Salinity: 32-34.0 psu										
	TAR			SB			BB				
	S	P	DC	S	SG	DC	S	P	SG	DC	S
Prorocentrales											
P. arenarium	×	×									
P. concavum	×	×		×		×	×	×	×	×	×
P. emarginatum	×	×		×			×			×	
P. faustiae	×										
P. foraminosum	×									×	
P. formosum	×										
P. lima	×	×	×	×	×	×	×		×		×
P. norrissianum											
P. rhathymum	×	×							×	×	
P. sculptile	×					×				×	×
P. sipadanensis sp. nov.											
Dinophysiales											
Sinophysis canaliculata	×	×									
S.microcephalus	×	×					×	×	×	×	
Sabahphysis squamosa gen. et sp. nov.											
Gonyaulacales											
Gambierdiscuspacificus				×							
Coolia tropicalis	×	×	×			×			×		
Ostreopsis labens	×	×			×						×
O. lenticularis	×		×				×				×
O. ovata	×		×	×	×			×			×
Gymnodiniales											
Amphidinium carterae											
A. operculatum	×	×		×						×	
Peridiniales											
Bysmatrum caponii	×	×					×	×			×
B. subsalsum											
*Peridinium quinquecorne**							×	×	×		
Incertae sedis											
Pileidinium ciceropse											
Total species identified		17			9			14			

valve view and valve pores of 0.14 μm diameter. The presence of marginal pores and the number of platelets at periflagellar area was not mentioned. However it appears that *P. arabianum* has 8-9 platelets (Morton et al. 2002; fig. 3). *Prorocentrum arabianum* is a planktonic species and produces cytotoxic and ichthyotoxic compounds, while *P. faustiae* is benthic and produces okadaic acid and dinophysis toxins (Morton 1998). Until further informations such as the toxicity and molecular data have been acquired, we tentatively identify our *Prorocentrum* as *P. faustiae,* but the two taxa need to be examined further. In *P. emarginatum*, we observed a pyrenoid, and this feature can therefore

BB=Bak-Bak Beach, MI= Mabul Island, SI=Sipadan Island), Sarawak (TD=Tanjung Datu, TS=Tanjung Serabang, PT=Talang dead coral, SG=seagrasses, H=*Halimeda* sp., RA=red algae, Sd=sand) and the total number of species identified at each sampling

25/02/03 (MI & SI)								Sarawak SD: 4/9/03 Salinity: 36.0 psu						Peninsula SD: 16/8/03 Salinity: 32-34.0 psu		
MI			SI		TD			TS					PT	PD		
P	SG	S	P	SG	S	P	DC	S	P	H	RA	DC	DC	S	Sd	DC
	×															
×	×	×	×	×	×											
		×	×	×												
×	×	×	×	×												
×	×	×	×	×	×	×		×		×				×	×	×
		×	×	×		×										
	×	×	×			×		×								
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					×											
					×											
×		×	×	×												
		×	×	×												
				×												
12		18			9			3					1	3		

be added as a species characteristic. In previous descriptions, a pyrenoid was not observed (Hansen et al. 2001) or not discussed (Fukuyo 1981, Faust 1990, and Faust et al. 1999).

Prorocentrum rhathymum from Malaysia possessed some morphological features of *P. mexicanum* (Cortés-Altamirano and Sierra-Beltrán 2003) such as trichocyst pores on both valves, a central pyrenoid and a posterior nucleus. The morphology and taxonomy of *P. mexicanum* discussed by Cortés-Altamirano and Sierra-Beltrán (2003) therefore need to be addressed in further detail. However, there is little doubt that *P. rhathymum* and *P. mexicanum* are separate species, and the placement of *P. mexicanum*

as a synonym of *P. rhathymum* by several authors such as Faust (1990) is not supported. The presence of *P. rhathymum* in Malaysia indicates that this species has a wide geographic distribution just as *P. mexicanum*.

Prorocentrum sipadanensis sp. nov. is a small benthic species, observed a few times at Sipadan Island. It differs clearly in morphology from other benthic *Prorocentrum* species (Balech 1956, Loeblich et al. 1979a, Fukuyo 1981, Faust 1990, 1991, 1993a, 1993b, 1994, 1997, Grzebyk et al. 1998, Morton 1998, Ten-Hage et al. 2000a). It coexists with other dinoflagellates and lives in association with seagrasses.

The thecal surface of *P. sipadanensis* posseses numerous shallow depressions, and similar depressions have been reported in *P. sculptile* (Faust 1994). The pores of *P. sipadanensis* are scattered on the valve surface. The pores are radially arranged in *P. rhathymum* (Loeblich et al. 1979a), *P sculptile* (this study) and *P. emarginatum* (Faust et al. 1999). The presence of marginal pores in *P. sipadanensis* is also a distinct species characteristic. Marginal pores have been previously reported in *P. lima* (Faust et al. 1999), *P. emarginatum* (Faust 1994) and *P. maculosum* (Faust 1993b). The periflagellar area of *P. sipadanensis* consists of 8 platelets as in several other benthic species (viz. *P. concavum* (Faust 1990), *P. maculosum, P. foraminosum* (Faust 1993b), *P. norrisianum, P. tropicalis* (Faust 1997), *P. lima* (Faust, et al. 1999) and *P. borbonicum* (Ten-Hage et al. 2000a)).

Prorocentrum sipadanensis is considered to be small benthic species. Several other small benthic *Prorocentrum* species have also been reported: *P. norrisianum* (Faust 1997), *P. borbonicum* (Ten-Hage et al. 2000a) and *P. elegans* (Faust 1993a). Small species of *Prorocentrum* are more common in plankton, e.g. *P. nanum, P. triestinum* and *P. minimum* (Dodge 1982), *P. balticum* (Steidinger & Tangen 1996), *P. venetum* (Tolomio & Cavolo 1985) and *P. nux* (Puigserver & Zingone 2002).

Order Dinophysiales

In this study, 2 species of *Sinophysis* (*S. canaliculata* and *S. microcephalus*) were identified. *Sinophysis canaliculata* is rounded, has a long and narrow depression on the left lateral view, and the sulcus length does not exceed 2/3 the length of the hypotheca. *Sinophysis microcephalus* is more elongate and the sulcus exceeds 2/3 the length of the hypotheca. Morphological features of the Malaysian material fit with previous descriptions. The two tropical species have an areolated surface while the temperate species (*S. ebriolum, S. stenosoma, S. grandis* and *S. minors*) have a smooth thecal surface (Saunders & Dodge 1984, Hoppenrath 2000b, Selina & Hoppenrath 2004). Recently, Selina and Hoppenrath (2004) re-examined the plate tabulation (especially the hypothecal plate) of the temperate *Sinophysis* species and compared them with the descriptions of Nie & Wang (1944) and Balech (1956). The new study agreed with the number of the hypothecal plates present (two lateral and two ventral plates) found by the early authors although this could not be demonstrated in all species studied.

Order Gonyaulacales

Only one species of *Gambierdiscus* (*G. pacificus*) was identified in our material. A comparison with the original descriptions of Chinain et al. (1999), showed our specimen to be smaller in size and the thecal surface is less smooth. Our material agreed in size with *G. belizeanus* (Faust, 1995) but differed in a less deeply areolated thecal surface. The widely distributed species *G. toxicus* was not observed but it has previously been reported from Malaysian waters (Lim et al. 2003).

Coolia sp. from Malaysia differs from *C. tropicales* by having a shorter Po (4-6 μm long) and plate 1" is the smallest precingular plate. *Coolia* sp. differs from two other species of *Coolia*, *C. monotis* and *C. areolata* by having less pores on the thecal surface plates 1', 3' and 2'"" are quadrangular and the length of the Po is 4-6 μm long versus 12 μm long in *C. monotis* and 9-10 μm long in *C. areolata* (Faust 1995, Ten-Hage et al. 2000c). *Coolia monotis* is the only known toxic species in the genus.

Ostreopsis is another genus that is commonly identified in tropical benthic environments. It differs from other dinoflagellates in the ventral plate having a ventral pore (Vo), and the presence of a ridged plate (Rp) in the cingulum (Faust et al. 1996). In this study, three species were observed, *O. labens, O. lenticularis* and *O. ovata*. Species of *Ostreopsis* are distinguished by shape and size of cells, shape and size of thecal plates and ornamentation of the thecal surface (Hansen et al. 2001). These criteria are difficult to apply, especially on cells in culture which often have somewhat aberrant morphology (Holmes et al. 1998). To provide better means of identification, field samples or young cultures are required. This is important because a few of *Ostreopsis* spp. (*O. mascarenensis* and *O. siamensis*; Lenoir et al. 2004 and Rhodes et al. 2000) have been found to produce palytoxin or palytoxin analogues which

may be responsible for clupeotoxism and other cases of toxicity (Lenoir et al. 2004).

Ostreopsis labens observed in this study possessed two sizes of pores. Only a few of the small size were observed and this may explain why they were not observed by Faust and Morton (1995). The thecal plate of *O. lenticularis* also had two sizes of pores but the small pores were more numerous compared to *O. labens*. Two different sizes of pores were also reported in *O. lenticularis* by Fukuyo (1981) and Hansen et al. (2001) but not by Faust et al. (1996). The morphological characteristics of *Ostreopsis ovata* fit with the taxonomic descriptions by other researchers such as Fukuyo (1981), Besada et al. (1982), Faust et al. (1996) and Hansen et al. (2001).

Order Gymnodiniales

In this order, two species from the family Gymnodiniaceae were identified (*Amphidinium carterae* and *A. operculatum). Amphidinium carterae* differs from *A. operculatum* in having smaller size, the presence of a central pyrenoid and the chloroplast lobes radiating toward the periphery. In *A. operculatum* the chloroplasts are located in the central part of the cell and more scattered near the cell periphery. A pyrenoid is absent (Murray et al. 2004a).

Order Peridiniales

Two species of the genus *Bysmatrum* (*B. caponii* and *B. granulosum*) were identified. The overall morphology of these two species fits with previous taxonomic descriptions. *Bysmatrum granulosum* differs from *B. caponii* in being larger and ornamented by wart-like projections on the thecal surface. *Bysmatrum caponii* has a reticulated thecal surface. Both species have 4-sided first anterior intercalary plate (1a) and 6-sided second anterior intercalary plate (2a).

Incertae sedis

Pileidinium ciceropse identified from Malaysia fit generally with the original description from Palau. However, our material showed a more highly reticulated thecal surface, and many of the polygonal shallow depressions were perforated by pores of various sizes. According to Tamura & Horiguchi (2005), the taxonomic position of this species is uncertain due to its higly modified thecal plate arrangement and poor bootstrap values of the SSU rDNA trees. In the study of Tamura & Horiguchi (2005), *P. ciceropse* formed a clade with *Amphidiniella sedentaria*, of Gonyaucales affinity. *Amphidiniella sedentaria* differs in the dorsiventrally compressed shape and in thecal plate arrangement. *Pileidinium ciceropse* shows similarity in hypothecal plate arrangement to *Cabra matta* (Murray & Patterson 2004) and *Plagiodinium belizeanum* (Faust & Balech 1993). These species possess both large postcingular plates 2''' and 4''', and more or less narrow postcingular plates 1''', 3''' and 5'''. No ornamentations such as flange or pointed bump were observed in *P. ciceropse*.

Pileidinium ciceropse possess an incomplete cingulum. Among the armoured dinoflagellates, this somewhat unusual feature is known also in *Hemidinium* Stein, *Crypthecodinium* Biecheler (Fensome et al. 1993), *Stylodinium littorale* Horiguchi et Chihara (Horiguchi & Chihara 1983), *Thecadinium dragesconii* Balech (Hoppenrath 2000c) and *Amphidiniopsis korewalensis* Murray et Patterson (Murray & Patterson 2002). These species, however all possess an additional 'x' plate on the right side of the sulcus. An 'x' plate was also described in *Cabra matta* (Murray & Patterson 2004). The taxonomic positions of all these genera are uncertain due to lack of ultrastructural, molecular data, life cycle, etc. (e.g. Fensome 1993). A comparison of the epithecal plate pattern in these genera showed disimilarities to *Pileidinium ciceropse* particularly in the absence of an apical pore, Po and intercalary plate. Most of the known benthic species have a complex epithecal plate arrangement except for *Plagiodinium*. Member of this genus possess a small sixth epithecal element (Po) and 5 apical plates while precingular plates are absent (Faust & Balech 1993).

Conclusions

Twenty four species of dinoflagellates were identified from Malaysian waters, many of them for the first time, including one previously undescribed species from Sipadan Island. This survey has documented that Malaysian waters have a diverse flora of marine benthic dinoflagellates. A long-term study may provide more accurate characterization of the benthic communities and provide more information about the distribution of the new species from Sipadan Island. The rich benthic flora of Sipadan Island supports the efforts of the Sabah Government to retain the island as a protected area. The finding of 8 potentially toxic species in

Malaysia indicates that Malaysia may encounter fish poisoning. The risk increases when new shellfish areas are added (Steidinger 1993), and the physical, chemical and biological factors that influence the blooming of the benthic species need to be assessed. Such factors are important for the setting up of monitoring and management programs of HAB species.

Morphological observations on the benthic species identified from Malaysia generally agreed with previous taxonomic descriptions from other geographical areas. Some new features were observed such as the presence of a pyrenoid in *P. emarginatum* and the presence of two different sizes of pores in *O. labens*. For routine monitoring programs, light microcscopy with epifluorescence is a convenient alternative to SEM.

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