IOC e-learning Course on Harmful Marine Microalgae

University of Copenhagen

Module 4

Benthic species of
Prorocentrum & Unarmoured Dinoflagellates

Available on Ocean Teacher on 24 July 2022,
on-line sessions to be announced

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Benthic species of *Prorocentrum*

Outline of module

Recommended reading for this module:

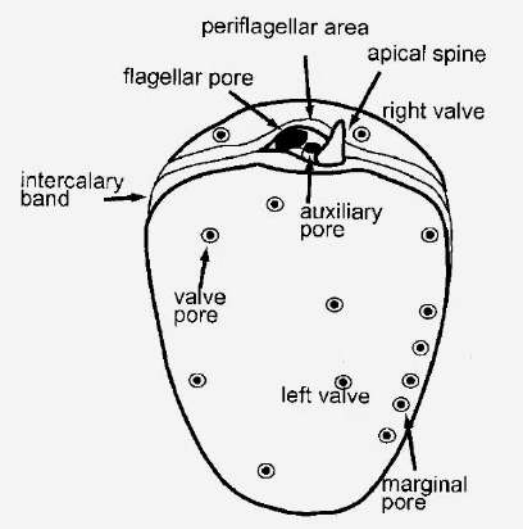
Chomérat, N., Bilien, G. & Zentz, F. 2019. A taxonomical study of benthic *Prorocentrum* species (Prorocentrales, Dinophyceae) from Anse Dufour (Martinique Island, eastern Caribbean Sea). – Marine Biodiversity 49: 1299-1319. – https://doi.org/10.1007/s12526-018-0913-6

Hoppenrath, M., Chomérat, N., Horiguchi, T., Schweikert, M., Nagahama, Y. & Murray, S. 2013. Taxonomy and phylogeny of the benthic Prorocentrum species (Dinophyceae) – A proposal and review. – Harmful Algae 27:1-28.

1.1 Identification of *Prorocentrum*

Species belonging to this order are composed of two large plates (or valves) and a number of small plates inserted anteriorly (the peri-flagellar area). The cells have two dissimilar flagella emerging from the flagellate pore.

The genus *Prorocentrum* Ehrenberg 1834 comprises 80 species. The type species is *P. micans* and it has been re-described from the type locality in the Baltic Sea. The genus is almost exclusively marine and is common in both pelagic and benthic habitats; only two species are found in freshwater habitats.



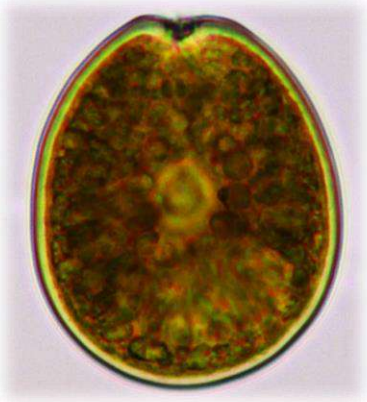
Many species of *Prorocentrum* can be identified in LM. The most important diagnostic features are

- Size, LM
- Shape, LM
- ± Spines, projections, LM (SEM)
- ± Pyrenoids, LM
- Fine structure of the valve and pores, LM/SEM
- Detailed structure of the periflagellar area, LM/SEM

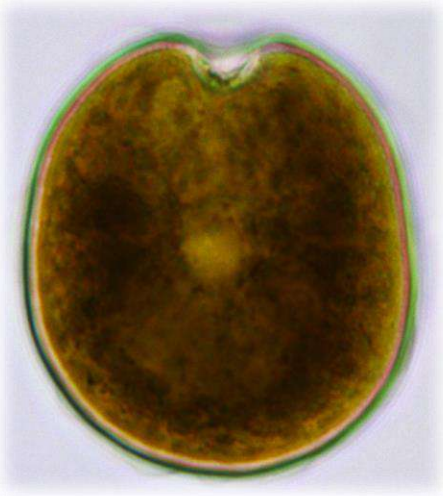
1.1 Identification of *Prorocentrum*

- **Size** – cell length does usually not include the spine length, sizes vary from 6-120 µm, most species are 30-50 µm long
- **Shape** – most species have flattened cells, but some are globular – the species may be divided into symmetrical and asymmetrical (around the longitudinal axis and this division is supported by molecular data, see slide xx below
- ± Spines, projections
- ± Pyrenoids
- Fine structure of the valve and pores
  - smooth ~ areolated
  - number and arrangement of valve pores
  - marginal pores
- Detailed structure of the periflagellar area

Symmetric species



P. lima



P. concavum

Asymmetric species

P. micans (type species)

P. emarginatum

P. rhathymum

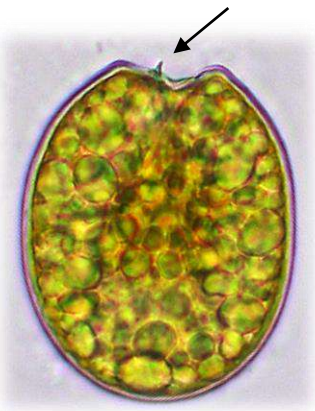
20 µm

All species shown to the same scale

1.1 Identification of *Prorocentrum*

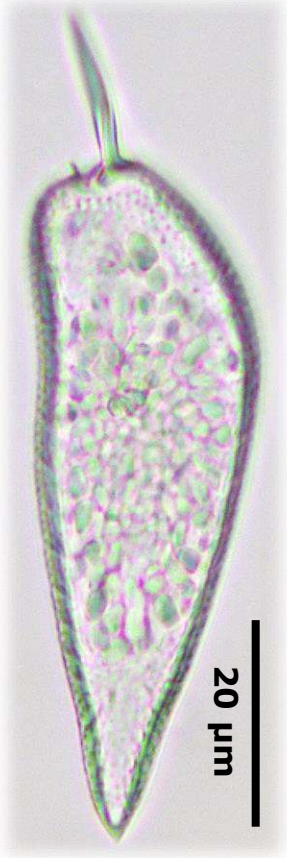
- Size
- Shape
- **± Spines, projections – conspicuous in many planktonic species – when present in benthic species, the spine is often (very) short and may be difficult to observe in LM, in some species the spine(s) is only visible in SEM**
- ± Pyrenoids
- Fine structure of the valve and pores
  - smooth ~ areolated
  - number and arrangement of valve pores
  - marginal pores
- Detailed structure of the periflagellar area

P. rhathymum
benthic species



P. emarginatum
benthic species

P. sigmoides
planktonic species



All species shown to the same scale, except the SEM image

1.1 Identification of *Prorocentrum*

- Size
- Shape
- ± Spines, projections
- **± Pyrenoids - all species of *Prorocentrum* have two chloroplasts located beneath the valves with or without pyrenoids - pyrenoids surrounded by starch sheath are usually conspicuous, but 'naked' pyrenoids without starch sheath may be difficult to observe, mostly found in benthic species,**
- Fine structure of the valve and pores
  - smooth ~ areolated
  - number and arrangement of valve pores
  - marginal pores
- Detailed structure of the peri-flagellar area

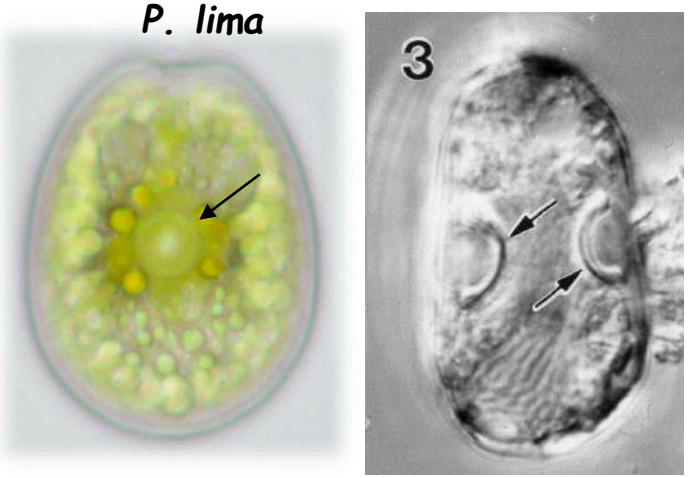
P. emarginatum

Observation of 'naked pyrenoids ' may be facilitated by epifluorescence microscopy

P. triestinum

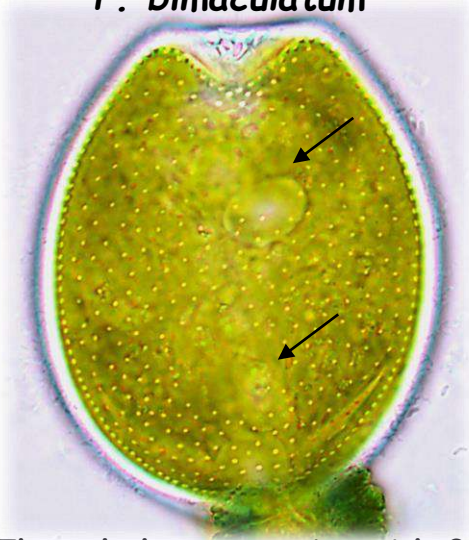
Planktonic species with 'naked' pyrenoid

P. lima



Pyrenoid with starch sheath, in lateral view (right) both pyrenoids are visible

P. bimaculatum



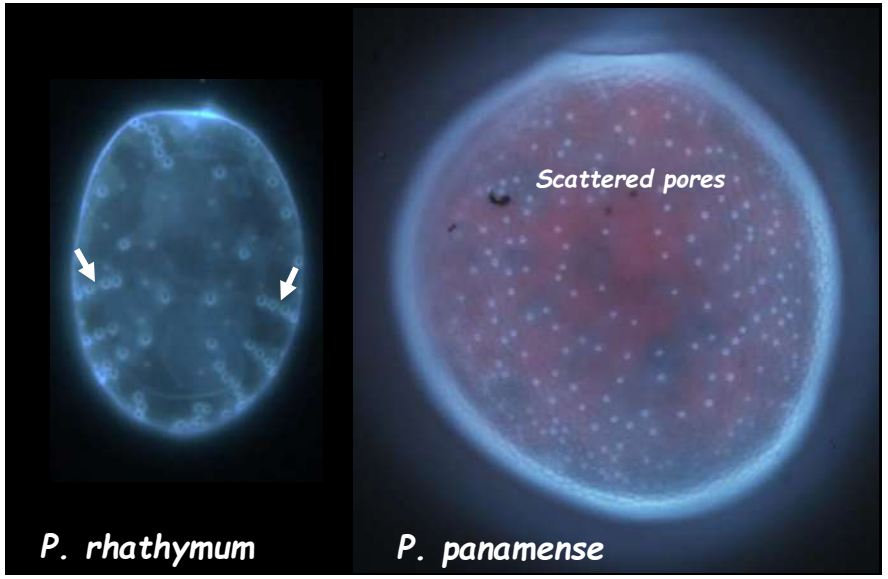
The only known species with 2 pyrenoids in each chloroplast

20 µm

All species shown to the same scale

1.1 Identification of *Prorocentrum*

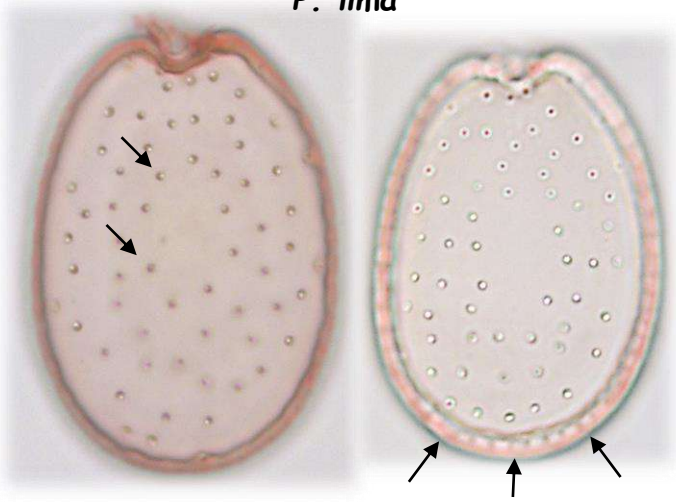
- Size
- Shape
- ± Spines, projections
- ± Pyrenoids
- **Fine structure of the valve and pores**
  - **smooth ~ areolated**
  - **number and arrangement of valve pores**
  - **marginal pores**
- Detailed structure of the periflagellar area



In some species pores are scattered on the valve while they form linear patterns in other species

P. hoffmannianum

P. lima

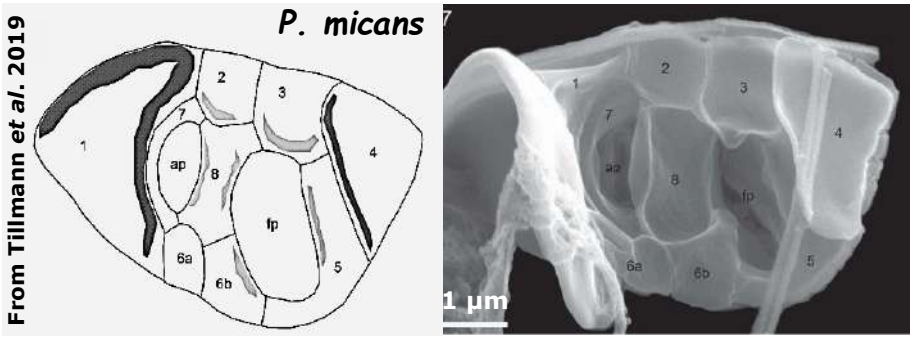


Valve smooth with scattered valve pores and marginal pores

All species shown to the same scale

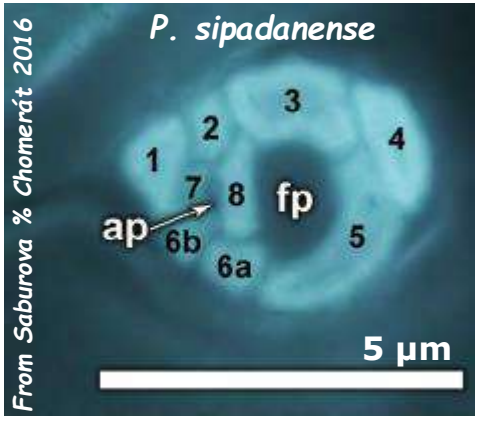
1.1 Identification of *Prorocentrum*

- Size
- Shape
- ± Spines, projections
- ± Pyrenoids
- Fine structure of the valve and pores
  - smooth ~ areolated
  - number and arrangement **of valve pores**
  - **marginal pores**
- **Detailed structure of the peri-flagellar area - the taxonomic importance of this feature is uncertain and further studies are needed for assessment. There are different inter-pretations of the terminology applied to the platelets in the peri-flagellar area, see Hoppenrath *et al*. 2013.**

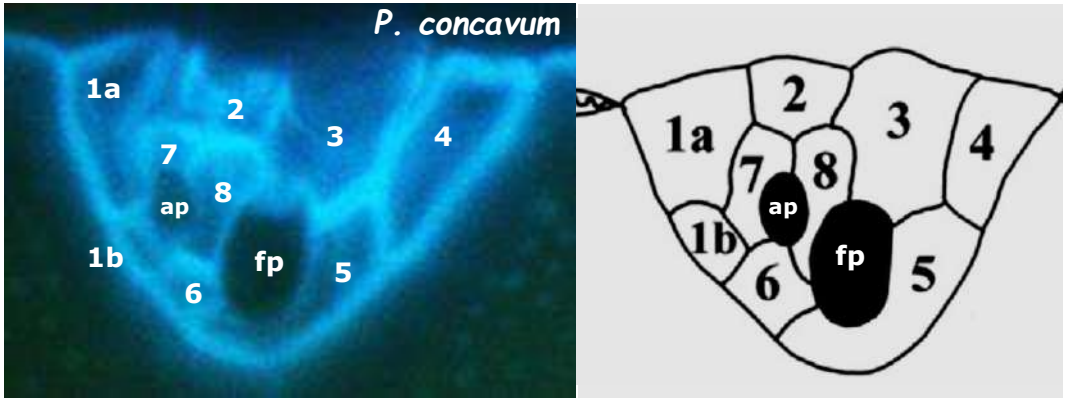


Peri-flagellar area of the type species, *P. micans*

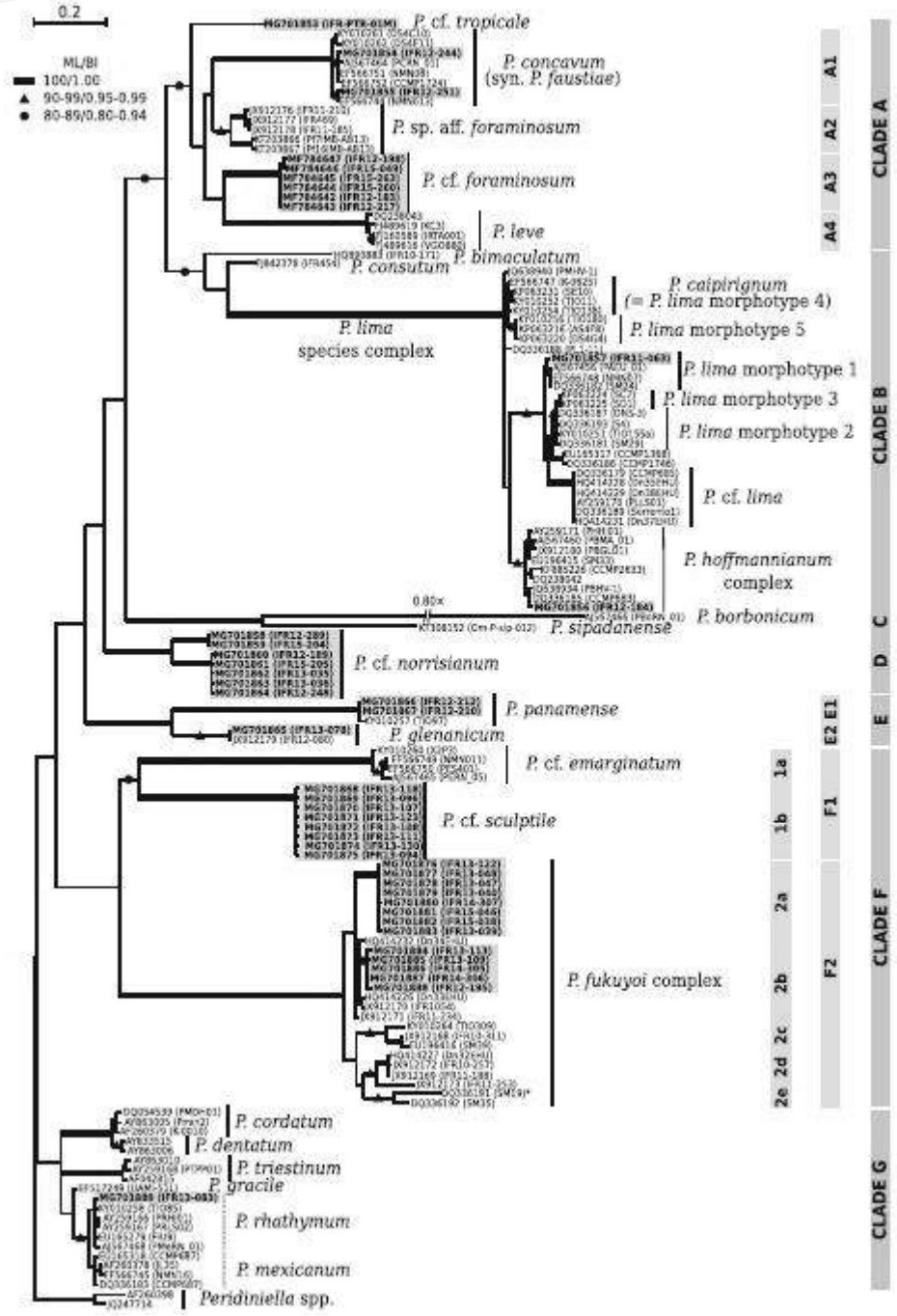
The tabulation of the peri-flagellar area is difficult to discern and there are conflicting reports in the literature on the structure of this in different species. Observation of the platelets usually requires SEM but in some species the platelets may be seen in LM.



The tabulation of the peri-flagellar areas is basically the same as in the type species, *P. micans*



In this species is plate 1 split into 1a and 1b, while plate 6 is not split and does not adjoin the auxiliary pore (ap) which is different to the type species, *P. micans*



1.2 Diversity of *Prorocentrum*

Chomérat *et al*. (2019) found that species of *Prorocentrum* formed 6 major clades, some with sub-clades.

Clade A. *P. concavum* and related species

Clade B. The *P. lima*-complex

Clade C. *P. borbonicum* and *P. sipadanense*

Clade D. *P. cf norrisianum*

Clade E. *P. panamense* and *P. glenanicum*

Clade F. The *P. emarginatum/fukuyoi* – complex

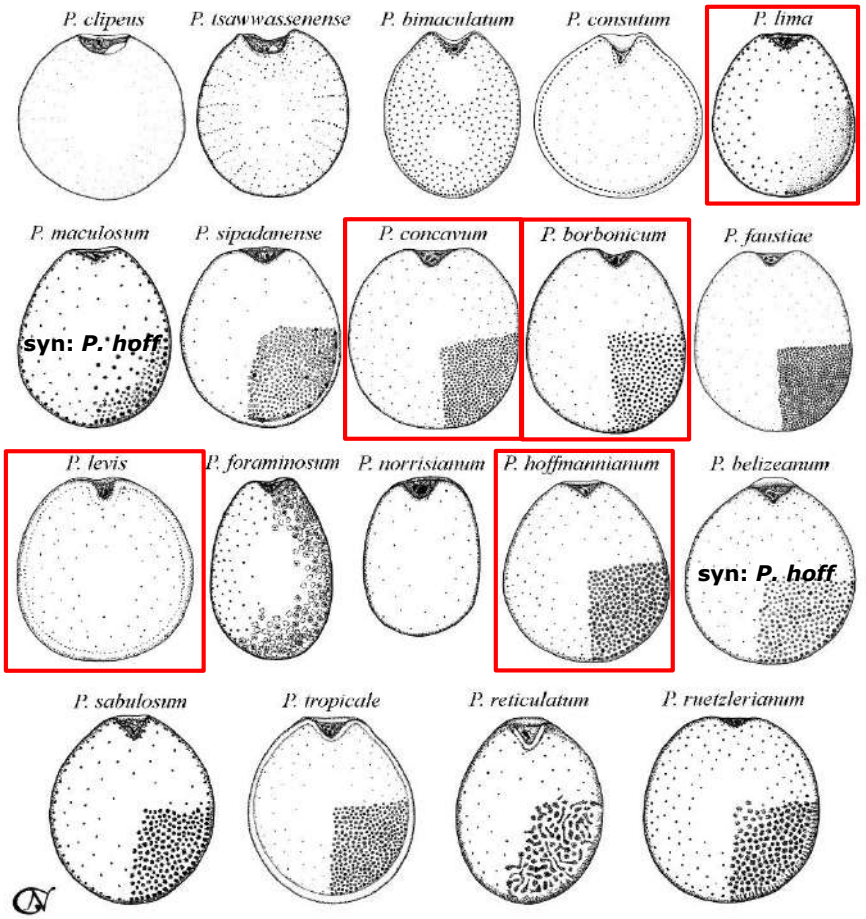
Clade G. *P. rhathymum* and planktonic species

In the following the species are grouped and illustrated according these clades. The clades indicated in red comprise toxic species.

1.2 Diversity of *Prorocentrum*

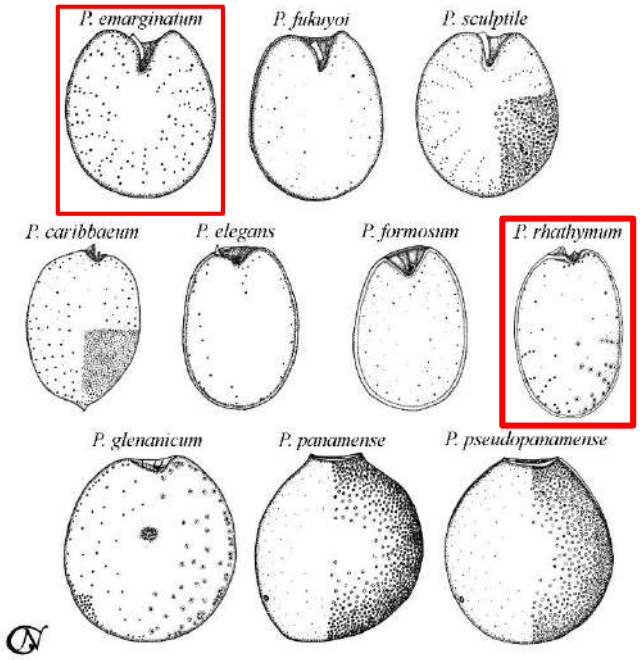
Benthic species of *Prorocentrum* may be divided into two groups (clades): symmetric species ~ asymmetric species. The red frames indicate the toxic species

Symmetric species



Identification of benthic species of *Prorocentrum* usually requires observation of details such as valve ornamentation and pores patterns. Therefore it is necessary to examine empty valves.

Asymmetric species



From Hoppenrath *et al*. 2013

1.2 Diversity of *Prorocentrum*

Prorocentrum

benthic species or species associated with substrates

Benthic species of *Prorocentrum* occur in many different habitats. They are often common, but usually not abundant. Some species are firmly attached to the substrate and move only occasionally, while other species are more active and move in the vicinity of the substrate.

- **Associated with seaweeds**
- **Attached to floating detritus**
- **Attached to corals**
- **Tide pools**
- **Sediments, sand-dwelling**

Benthic species of *Prorocentrum* which are potential toxin producers are high-lighted in yellow.

Information from Algaebase - Guiry, M.D. & Guiry, G.M. 2022 and Lundholm et al.

on 2020-11-14. doi:10.14284/362

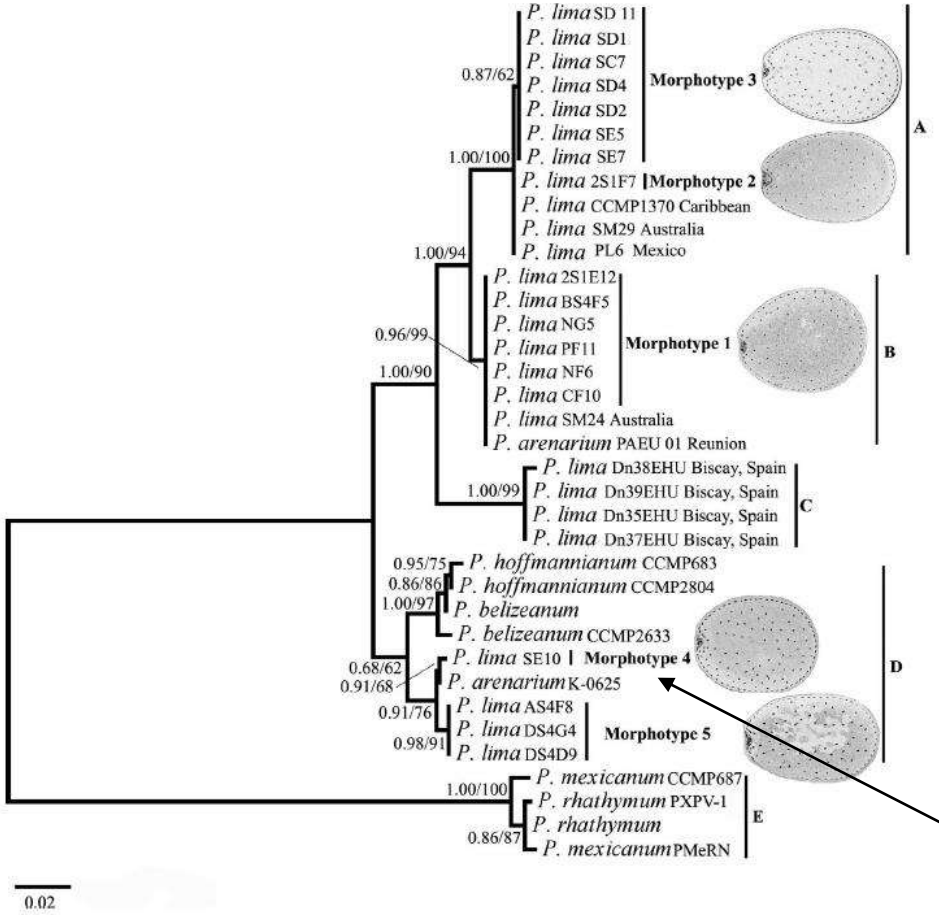
P. bimaculatum Chomerat *et* Saburova 2012	Chomerat *et al.* (2012)
P. borbonicum Ten-Hague *et al.* 2000	Ten-Hague *et al.* (2000)
P. caipirignum Fraga, Menezes *et* Nascimento 2017	Nascimento *et al.* 2017
P. carribaeum Faust 1993	Faust (1993a)
P. clipeus Hoppenrath 2000	Hoppenrath (2000)
P. concavum Fukuyo 1981 syn: ***P. arabianum*** Morton *et* Faust 2002	Fukuyo (1981), Faust *et al.* (1999), Taylor *et al.* (2004)
P. consutum Chomerat *et* Nezan 2010	Chomerat *et* Nezan (2010)
P. elegans Faust 1993	Faust (1993a)
P. emarginatum Fukuyo 1981	Fukuyo (1981), Faust *et al.* (1999), Taylor *et al.* (2004)
P. faustiae Morton 1998	Morton (1998)
P. foraminosum Faust 1993	Faust (1993b), Faust *et al.* (1999)
P. formosum Faust 1993	Faust (1993b)
P. fukuyoi Murray *et* Nagahama 2007	Murray & Nagahama (2007)
P. glenanicum Chomérat *et* Nézan 2011	Chomérat & Nézan (2011)
P. hoffmannianum Faust 1990 syn: ***P. belizeanum*** Faust 1993, ***P. maculosum*** Faust 1993	Faust (1990), Faust *et al.* (1999), Taylor *et al.* (2004)
P. leve Faust, Kibler, Vandersea, Tester *et* Litaker 2008	Faust *et al.* (2008), Aligizaki *et al.* (2009)
P. lima (Ehrenberg) Dodge 1975 (complex) syn: ***P. arenarium*** Faust 1994	Faust *et al.* (1999), Taylor *et al.* (2004), Nascimento *et al.* 2017
Prorocentrum malayense Lim, Leaw *et* Lim 2019	Lim *et al.* (2019)
P. mexicanum Osorio-Tafall 1942	Cortes-Altamirano & Sierra-Beltran (2003)
P. norrisianum Faust 1997	Faust (1997)
P. panamense Grzebyk *et al.* 1998	Grzebyk *et al.* (1998)
P. pseudopanamense Chomérat *et* Nézan 2011	Chomérat & Nézan 2011
P. reticulatum Faust 1997	Faust (1997)
P. rhathymum Loeblich *et al.* 1979	Faust *et al.* (1999) (as ***P. mexicanum***), Cortes-Altamirano & Sierra-Beltran (2003), Taylor *et al.* (2004)
P. ruetzlerianum Faust 1990	Faust (1990), Faust *et al.* (1999)
P. sabulosum Faust 1994	Faust (1994)
P. sculptile Faust 1994	Faust (1994)
P. sipadanensis Mohammad-Noor, Daugbjerg *et* Moestrup 2007	Mohammad-Noor *et al.* (2007)
Prorocentrum steidingerae Gómez, Qiu *et* Lin 2017	F.Gómez, D.Qiu & S.Lin 2017: 675, fig. 6c,d
P. tropicalis Faust 1997	Faust (1997)
P. tsawwassenense Hoppenrath *et* Leander 2008	Hoppenrath *et* B. S. Leander (2008)
P. vietnamensis Yoo *et al.* 2004	Yoo *et al.* (2004)

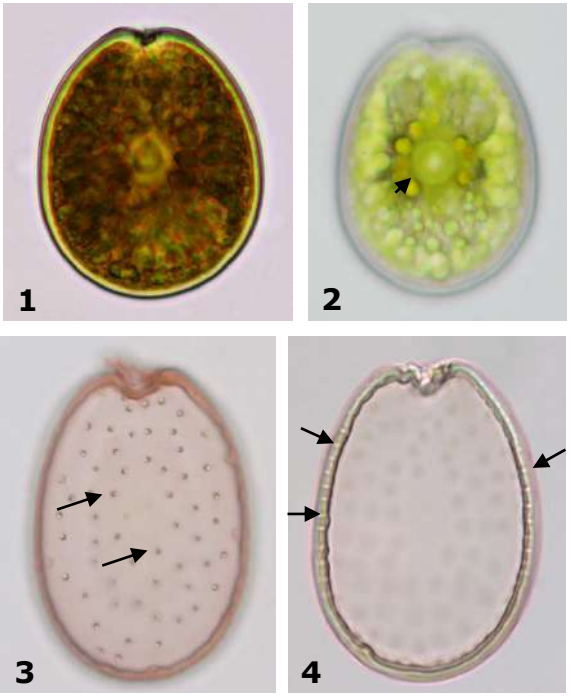
1.3 Common species of *Prorocentrum*

The *Prorocentrum lima* – complex (Clade B sensu Chomérat *et al*. 2019)

Prorocentum lima **is one of the most common benthic *Prorocentrum* species. It is cosmopolitan in temperate-tropical waters and usually 'easy' to identify. However, recent studies including molecular analyses have shown that *P. lima* is a species complex with 5 or even more genetically distinct species (Zhang *et* al. 2015, Nascimento *et al*. 2017).**

From Zhang *et al*. 2015



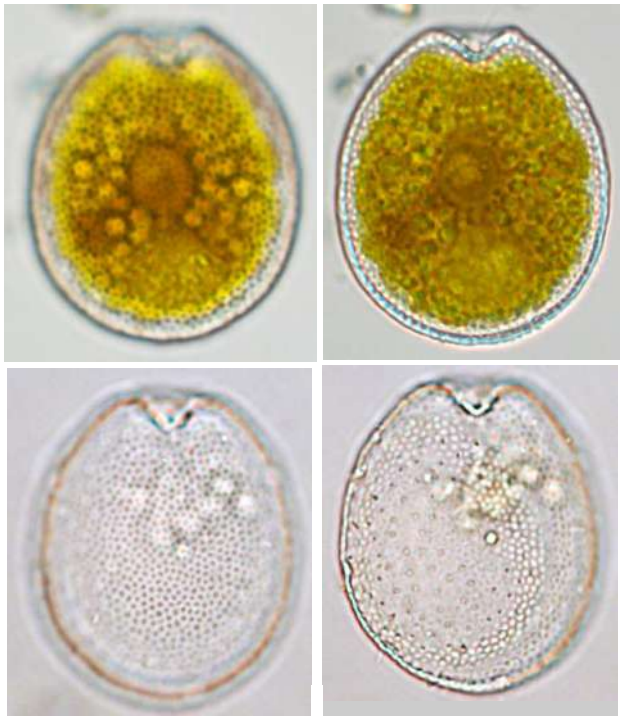


- Size: 35-57 µm long
- Symmetrical, shape variable, more or less ovate
- Pyrenoid present (Fig. 2, arrow head)
- Valve smooth, scattered pores except in centre, marginal pores present (Figs 3-4, arrows; same cell in different focus)
- Cosmopolitan, temperate-tropical areas
- Potentially toxic

Morphotype 4 is described as a new species, *P. caipirignum* Nascimento *et al*. (2017)

1.3 Common species of *Prorocentrum*

Prorocentrum hoffmannianum Faust 1990 (Clade B sensu Chomérat *et al*. 2019)

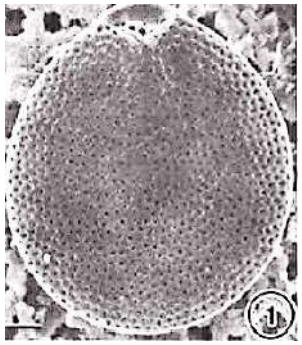


- Symmetrical, ovoid, 45-55 µm long
- Large central pyrenoid
- Valves with deep areolae, with scattered pores, note that only some areolae have pores, Fig. 5, arrows
- Marginal pores
- Tropical
- Toxic

The original descriptions of several benthic species of *Prorocentrum* are by SEM only and without cultures available. This means that intra- as well as interspecific variability is poorly known in most of these species.

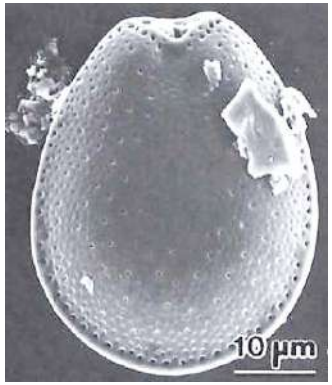
Thus, subsequent studies of *P. belizeanum* and *P. maculosum* including molecular analyses have shown that these species should be considered synonymous with *P. hoffkannianum* (Herrera-Sepúlveda *et al*. 2015, Rodríguez *et al*. 2018).

***P. belizeanum* Faust 1993**

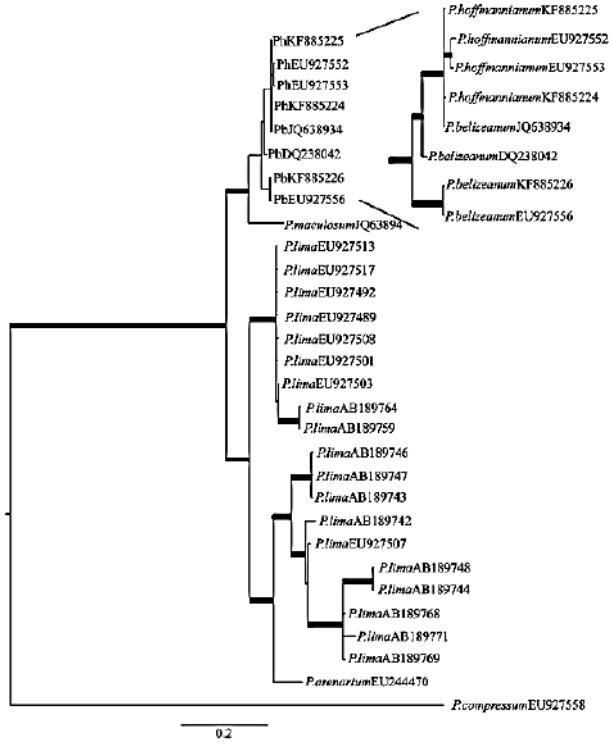


Holotype: Faust 1993a, Fig.1

***P. maculosum* Faust 1993**



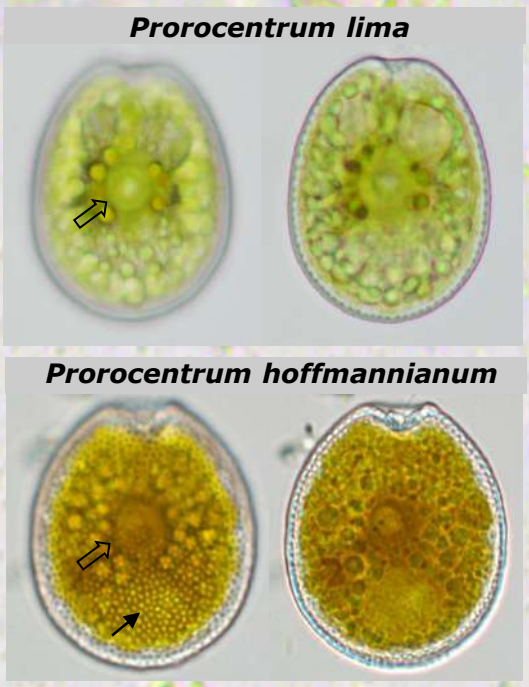
Holotype: Faust 1993b, Fig.1



From Herrera-Sepúlveda *et al*. 2015

Courses_Photos\Cultures\P.hoffmannianum-kwi\P.hoff1f,h,j,4a,7a,d

1.3 Common species of *Prorocentrum*



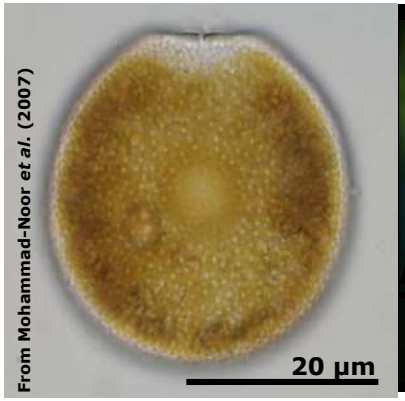
P. lima ~ *P. hoffmannianum*

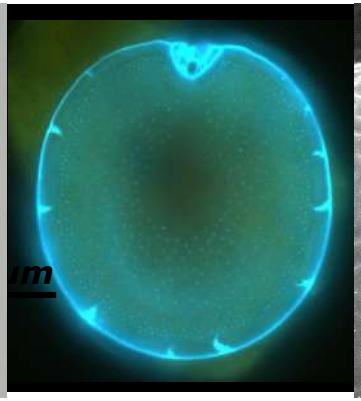
In samples from tropical sites, *P. lima* and *P. hoffmannianum* may occur together.

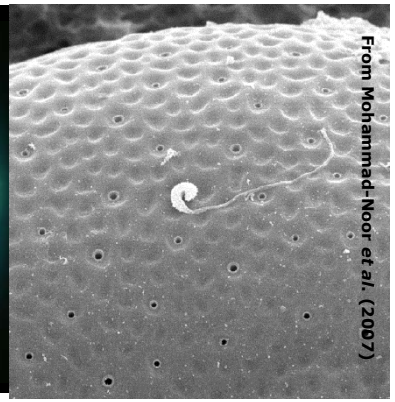
The background image is a micrograph with an inverted microscope (20x lens) and shows two cells of *P. hoffmannianum* and one cell of *P. lima*. If not examined carefully these species may be confused. Both species have pyrenoids, scattered valve pores and marginal pores, but are distinguished by the areolated valve surface in *P. hoffmannianum*, see inset and Slides 8, 10.

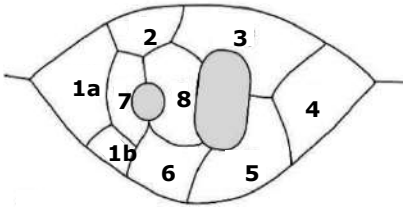
1.3 Common species of *Prorocentrum*

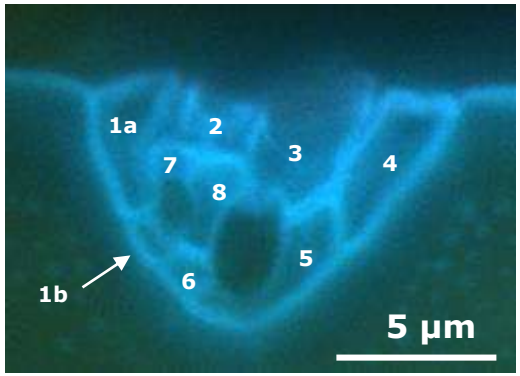
Prorocentrum concavum Fukuyo 1981 (Clade A sensu Chomérat *et al*. 2019)

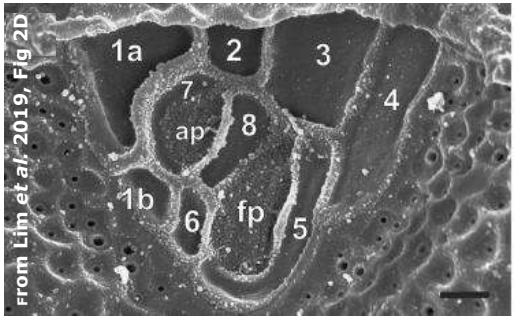




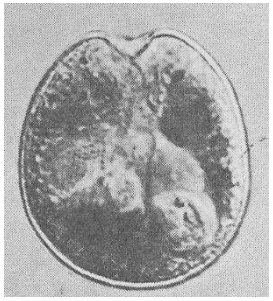








- Broad ovate, symmetrical, 45-55 µm long
- Pyrenoid present, without starch sheath
- Valves areolated, with many pores of two different sizes, the pares are surrounded by a shallow rim, the centre void of pores – the areolae are usually shallow and may be difficult to observe in LM
- Widely distributed in subtropical and tropical benthic habitats
- Potentially toxic



HOLOTYPE

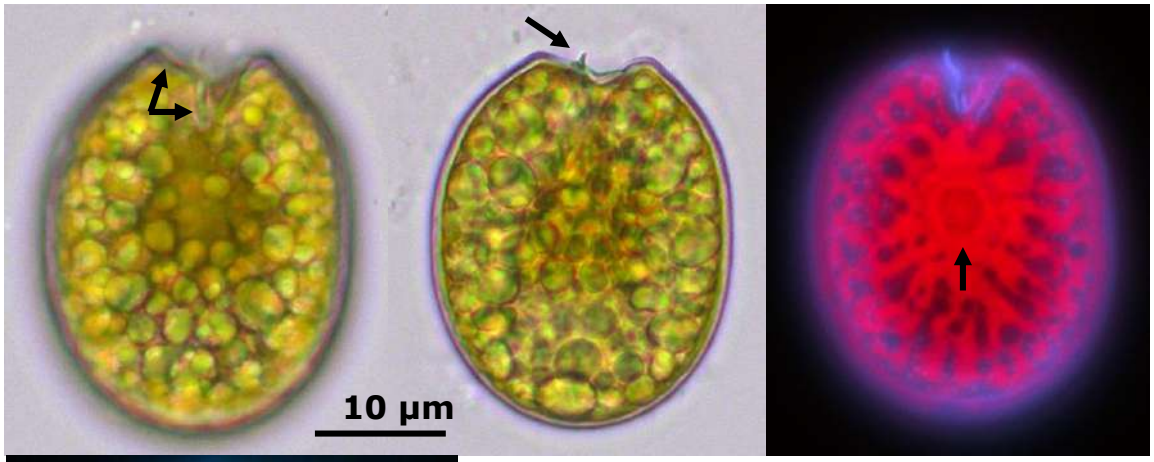
Prorocentrum concavum **was described from the tropical Pacific (Fukuyo 1981, Fig. 13).**

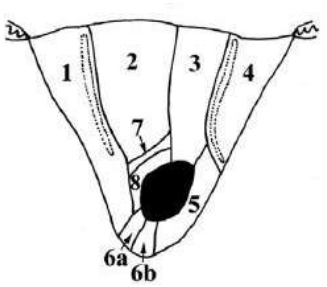
Mohammad-Noor *et al.* (2007b) re-investigated the original culture of *P. arabianum* Morton *et* Faust 2002 (CCMP 1724) and concluded that it is synonymous with *P. concavum*.

The peri-flagelllar area of *P. concacum* is composed of 9 platelets with platelet 1 split into two, 1a + 1b (Mohammad-Noor *et al*. 2007b, Hoppenrath *et al*. 2013, Lim *et al*. 2019).

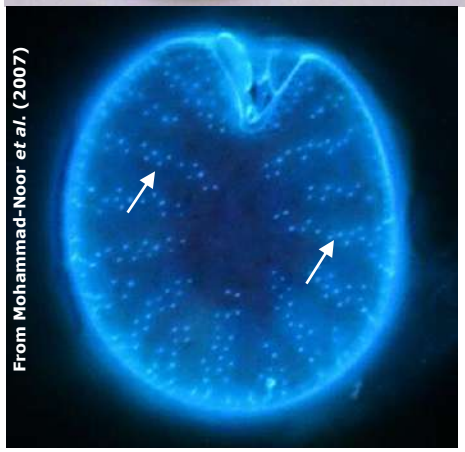
1.3 Common species of *Prorocentrum*

Prorocentrum emarginatum Fukuyo 1981 (Clade F sensu Chomérat *et al*. 2019)

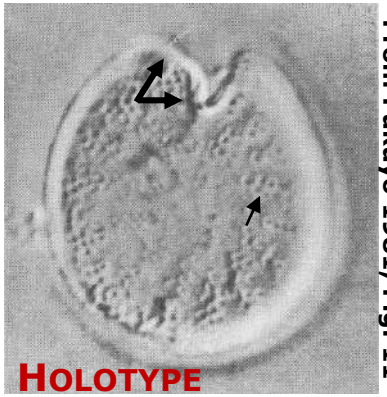




Drawing from Hoppenrath *et al.* 2013

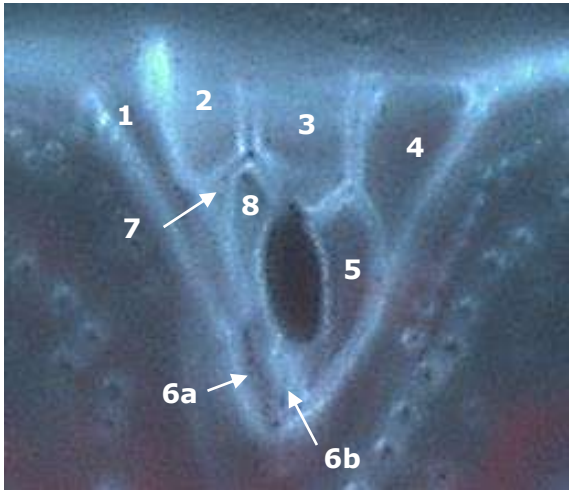


From Mohammad-Noor *et al.* (2007)



HOLOTYPE

From Fukuyo 1981, Fig. 11



An accessory pore seems to be absent in *P. emarginatum* but further studies are needed to confirm this.

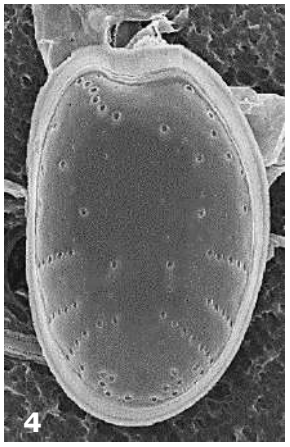
- Asymmetrical, round-oval, 30-40 µm long
- Pyrenoid present, without starch sheath
- Valves smooth, with small pores in 2-3 irregular rows forming linear patterns, fine marginal pores present
- Peri-flagellar area narrow V-shaped, with short spine
- Widely distributed in subtropical and tropical benthic habitats
- Toxic

This species is related to the non-toxic *P. fukuyoi* – it may be distinguished by the more rounded shape and the linear patterns formed by the valve pores. The two species may be synonymous.

1.3 Common species of *Prorocentrum*

Prorocentrum rhathymum Loeblisch *et al.* 1979 (Clade G sensu Chomérat *et al.* 2019)

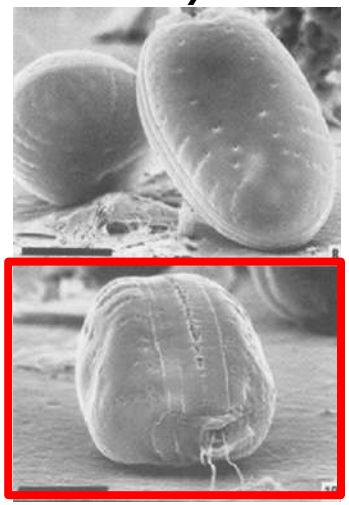
Figs 1-4 from Mohammad-Noor et al. 2005



- Size: 28-40 µm long
- Asymmetrical, oval, with small apical tooth (Fig.1, arrow head)
- Pyrenoid present, but without starch (Fig. 1, arrow)
- Valves smooth, with two types of pores; large pores forming bending lines particularly in the posterior end of the cell, LM; smaller pores are scattered randomly on the valve, SEM (LM)
- Widely distributed in warm temperate-tropical benthic habitats
- Potentially toxic

The identity of this species has been confused by misidentifications in the literature where it has been called *P. mexicanum*. Recently, Gomez *et al*. (2017) have argued *P. rhathymum* and *P. mexicanum* are synonymous, but consulting the original (type) descriptions of these species they appear to be clearly different and should be regarded as separate species (see Moestrup 2020, for further details).

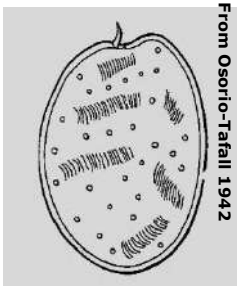
P. rhathymum



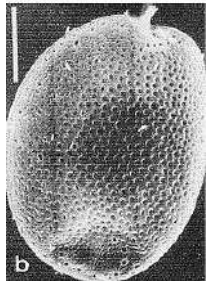
From Loeblich *et al*. 1979

HOLOTYPE

P. mexicanum



From Osorio-Tafall 1942



From Cortés-Altamirano & Sierra-Beltrán 2003

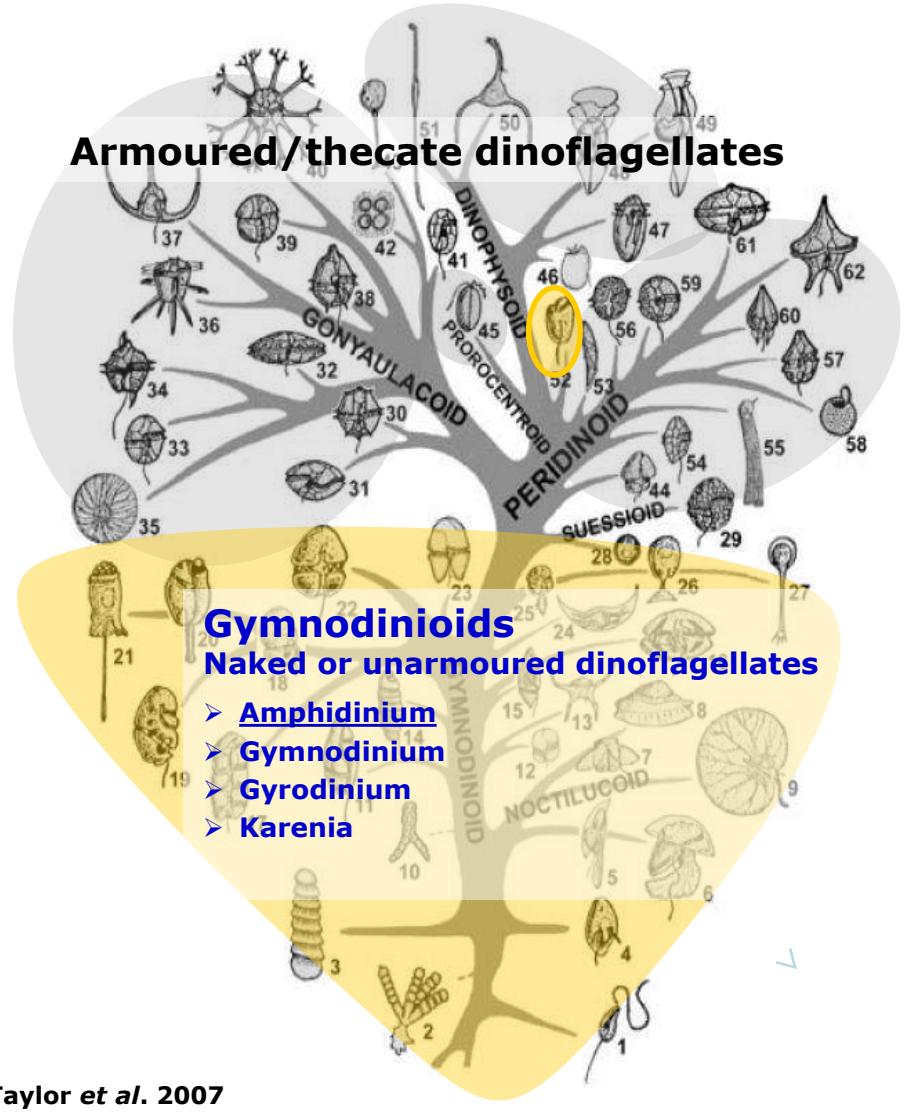
The original description of *P. rhathymum* was illustrated by SEM images, and clearly showed short bending lines of valve pores (Loeblich *et al*. 1979).

***P. mexicanum* was described by Osario-Tafall (1942) and his illustration did not indicate lines of pores; and neither did the re-description of this species by Cortés-Altamirano & Sierra-Beltrán (2003). According to the latter authors, *P. mexicanum* is a planktonic species while *P. rhathymum* is benthic.**

Gomez *et al*. (2017) described a third species, *P. steidingerae,* with valve pores similar to *P. rhathymum* but with rugose valve surface. This species is currently regarded synonymous with *P. rhathymum* (Moestrup 2020).

2.1 Identification of unarmoured dinoflagellates

Dinophyceae



From Taylor *et al*. 2007

The unarmoured dinoflagellates comprise almost one third (600-700) of the known species of dinoflagellates. Taxonomically, they are assigned to the class Dinophyceae with two orders, and the class Noctilucophyceae with one order.

Many species of unarmoured dinoflagellates do not retain the morphological characteristics used for identification in preserved samples. As a consequence, identification to the species level or even genus level is often difficult or impossible in preserved material, and particularly small species are presumably often misidentified and/or widely unrecognized in field surveys, see also Module 1.

2.1 Identification of unarmoured dinoflagellates

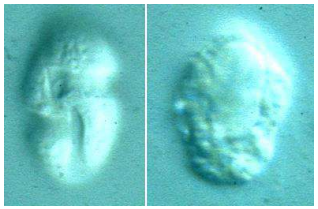
Several species appear to be described based on preserved material, and most of these description are not sufficiently detailed for the species to be identified. However, many descriptions are valid according to the ICN (International Code of Nomenclature) and therefore need to be considered in taxonomic accounts/ reviews. Such species names are sometimes referred to as 'bibliographic ghosts'.

Bibliographic ghosts

- Can never be identified on basis of their original description/illustration
- Disregard such names and describe new species
- Synonymize them with known, well-described species
- Give them an identity through emended descriptions

From Schiller 1933

Fig. 420. *Gymnodinium punctatum* Pouchet. Nach Pouchet.



The same cell after observation for 3 min under the LM. When cells are squashed or preserved, they loose their morphological features.

Practical identification

- Size and shape
- Position of structure of girdle and sulcus (displacement, overhang)
- Apical groove (often difficult to observe and not always visible in LM)
- Surface striations
- Presence/absence of chloroplasts, shape of chloroplasts, ± pyrenoid
- Other organelles, nucleus and its position in the cell, ± nematocysts, ± ocelli, ± peduncle

LIVE MATERIAL USUALLY NEEDED FOR CRITICAL IDENTIFICATION

SEM AND/OR MOLECULAR DATA ARE NEEDED IN SOME CASES

2.2 Diversity of *Amphidinium*

Amphidiniales Moestrup et Calado 2018 – 101 spp

The order Amphidiniales comprises only one genus *Amphidinium* and includes both photo- hetero-, and mixotrophic species. Their most characteristic feature is the cingulum which is located near the anterior end of the cell, typically V-shaped on the ventral side. Most species (all species?) occur in benthic habitats. Only four species are recogized as toxic according to the IOC Taxonomic Reference List.

Amphidinium carterae Hulburt 1957

Amphidinium gibbosum (Maranda *et* Shimizu) Jørgensen *et* Murray 2004

Amphidinium klebsii Kofoid *et* Swezy 1921

Amphidinium operculatum Claparède *et* Lachmann 1859

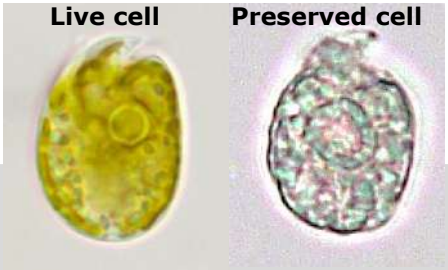
More than 180 species of benthic dinoflagellates belonging to about 40 genera are recorded from benthic habitats (Hoppenrath *et al*. 2014 and https://www.algaebase.org/).

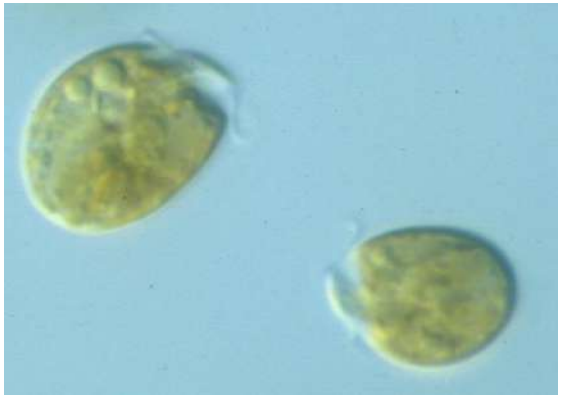
Species of *Amphidinium* as well as species previously assigned to this genus but now transferred to other new genera, are common in benthic habitats. Many species are common but occur often in low numbers, see also Module 2.

Amphidinium sensu lato

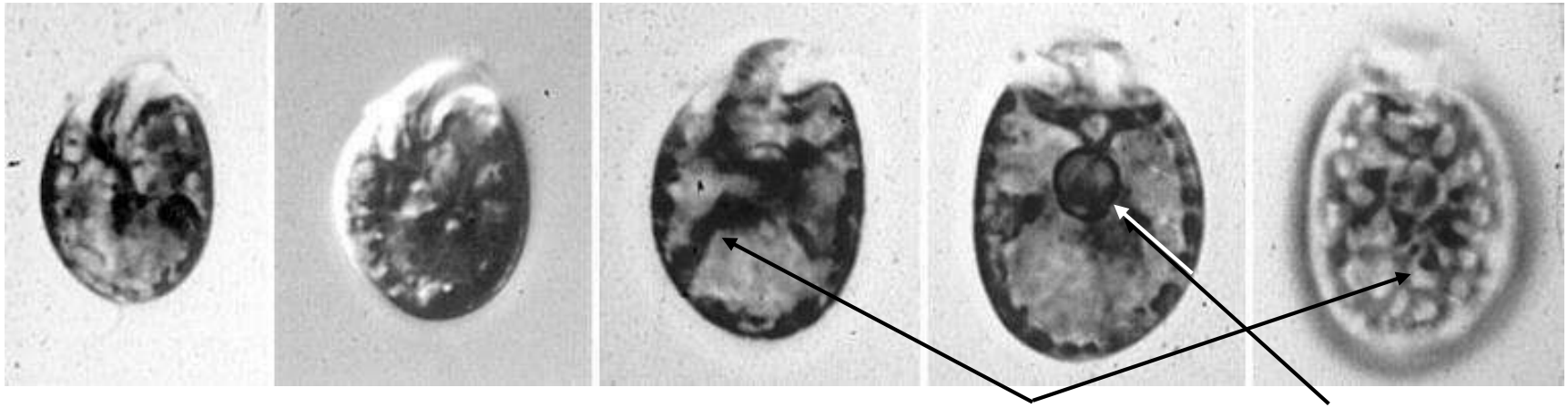
2.2 Diversity of *Amphidinium*

Amphidinium carterae Hulburt 1957





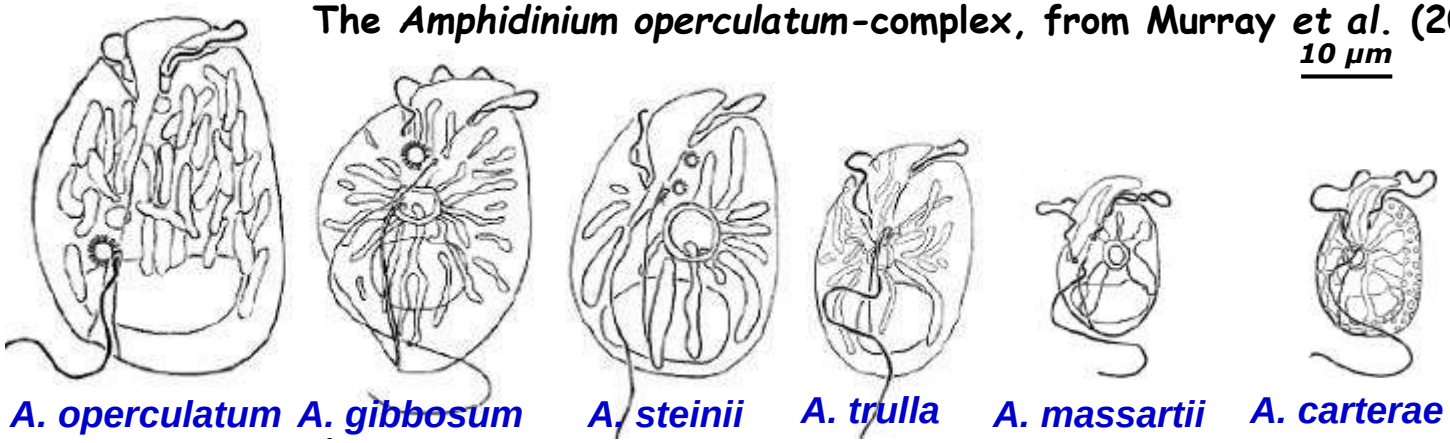
- 12-18 µm long
- One widely branched chloroplast with a central pyrenoid
- Potentially toxic
- Widely distributed, probably a cosmopolitan species – and it seems to be the most common species of Amphidinium and benthic habitats



One widely branched chloroplast with a central pyrenoid

2.2 Diversity of *Amphidinium*

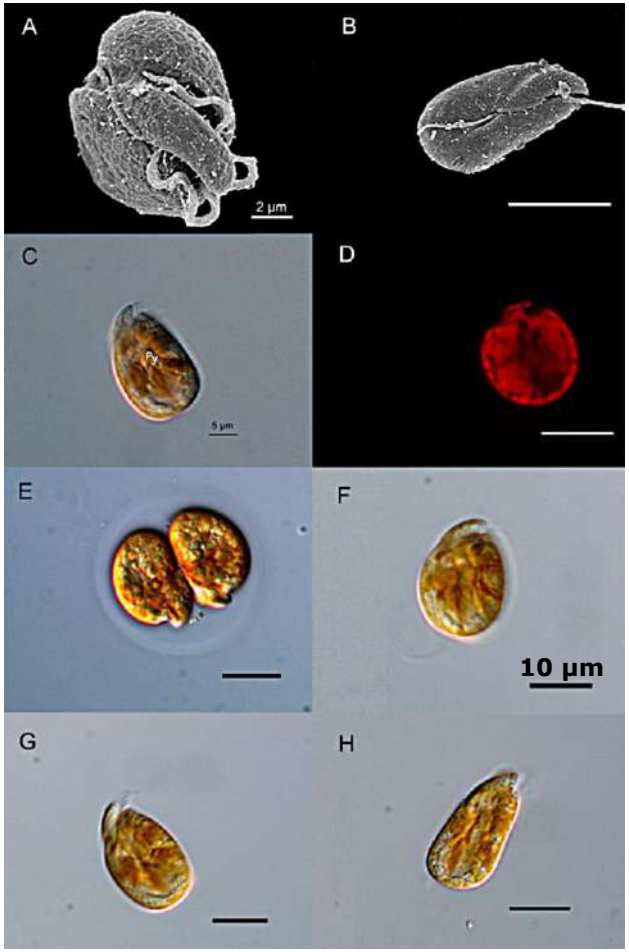
The *Amphidinium operculatum*-complex, from Murray *et al.* (2004)



	General cell shape	Position of origin of the sulcus	Position of distal end of the cingulum	Asexual division	Starch-sheathed ring-shaped pyrenoid	Form of the plastid
Amphidinium carterae	Oval	Close to the cingulum	0.5 of the cell length from the apex	In motile cells	Present	Single, lobes radiating, and superficial with perforations
Amphidinium gibbosum	"Hump-backed," with a pointed antapex	Close to the cingulum	0.3 of the cell length from the apex	In motile cells	Present	Single, strands radiating from the center
Amphidinium operculatum	Oval to pear shaped	Far from the cingulum, in the lower 1/3 of the cell	0.1–0.2 of the cell length from the apex	In motile cells	Absent	Appear to be multiple, elongated, scattered
Amphidinium massartii	Oval	Close to the cingulum	0.5–0.6 of the cell length from the apex	In motile cells	Present	Single, lobes radiating from the center
Amphidinium steinii	Oval, some cells can move metabolically and change their shape	Close to the cingulum	0.3–0.4 of the cell length from the apex	In cysts	Present	Single, strands radiating from the center
Amphidinium trulla	Oval	Close to the cingulum	0.3–0.4 of the cell length from the apex	In motile cells	Present	Single, lobes radiating from the center

2.2 Diversity of *Amphidinium*

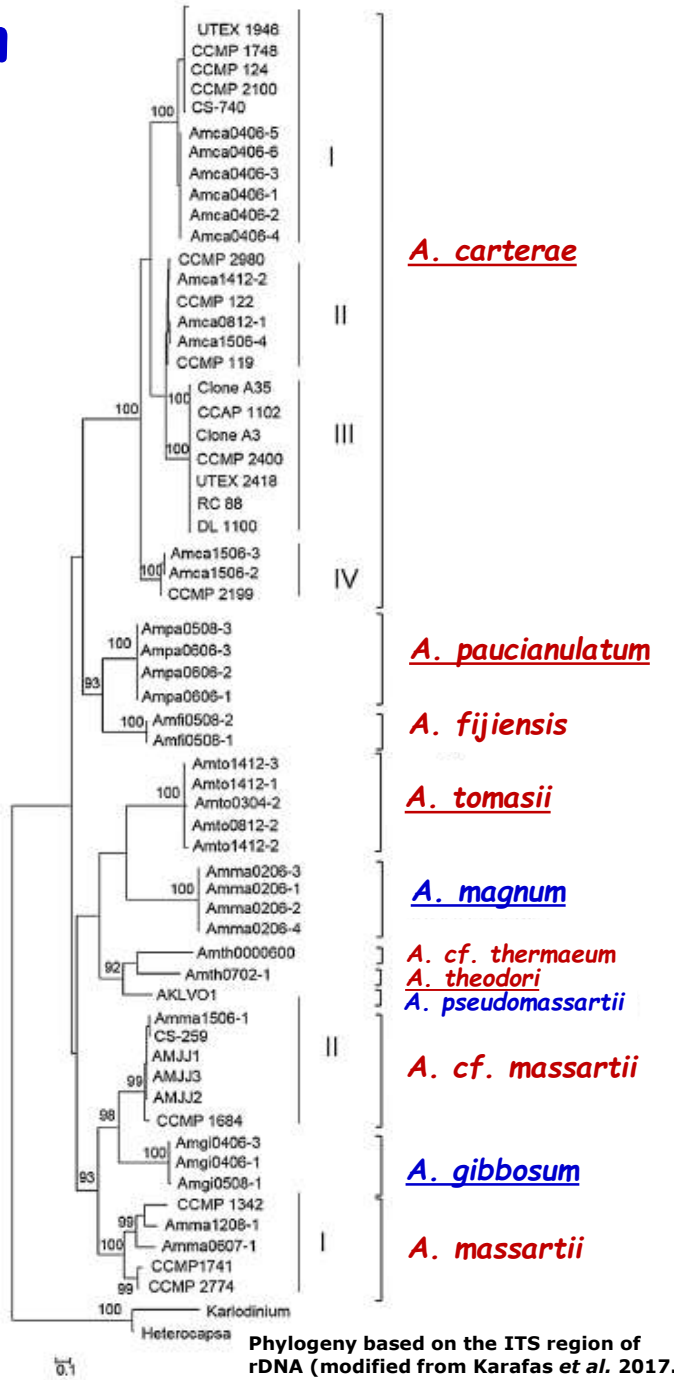
Karafas *et al*. (2017) described 6 new species in the *Amphidinium operculatum*-complex, notably *A. fijiensis, A. magnum, A. paucianulatum A. pseusomassartii, A. theodori, A. tomasii*. Species indicated in red in the phylogeny occur in the South Pacific; potentially toxic species are underlined.



Amphidinium fijiensis

***Amphidinium carterae, fijiensis, A. massartii, A.* cf. *massartii, A. paucianulatum, A. theodori* and *A.* cf. *thermaeum* have been described or reported from the tropical South Pacific (*A. fijiensis* has only been collected from a fish tank containing "live rock" imported from Korotoga Fiji).**

From Karafas *et al.* 2017



Phylogeny based on the ITS region of rDNA (modified from Karafas *et al.* 2017.

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