

First Record of The Thecate Marine Dinoflagellate *Protooperidinium abei* (Peridinales, Dinophyceae) in Indonesia

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ARTICLE INFO

Article history:

Received April 14, 2022

Received in revised form July 20, 2022

Accepted July 25, 2022

KEYWORDS:

Biodiversity,
Dinoflagellate,
Marine microalgae,
Protooperidinium abei,
Systematics,
Thecal plates

ABSTRACT

Two identical dinoflagellate cell specimens were found in a seawater sample collected from Tanjung Pasir Beach (TPB; 6.01 S, 106.8 N), Banten, Indonesia and subjected to morphological characterization light microscopy (LM). The cells measured 71.97–72.86 μm long and 52.55–52.76 μm wide, fusiform or biconical-shaped, with tapered apical and antapical horns. A sharp and pointy spine was present at the antapex. The Kofoidian thecal plates arrangement pattern of the specimens was formulated as Po, 4', 2a, 7'', 3(?)c, 4s, 5''', 2'''''. Based on this thecal plate tabulation formula combined with the cell morphologies, the specimens conformed to the original description of, and therefore identified as, *Protooperidinium abei* (Paulsen) Balech. This study constitutes the first record of *P. abei* in Indonesia and the first to illustrate and describe its detailed morphology using LM.

1. Introduction

The dinoflagellates represent one of the most diverse, complex, and abundant eukaryotic microalgae that play crucial ecological roles in aquatic ecosystems (Le Bescot *et al.* 2016; Taylor *et al.* 2008). They are distinguished from other microalgae lineages by a set of unique features like the presence of two distinct flagella (i.e. the transverse and longitudinal flagella), pigmentations (e.g. peridinin, dinoxanthin), specific organelles (e.g. the pusule, numerous) types of eyespots and its nucleus (i.e. the dinokaryon), among others (Fensome *et al.* 1993; Hackett *et al.* 2004; Taylor *et al.* 2008).

Some dinoflagellate genera possess cellulosic 'armour' plates (i.e. thecae) positioned within the amphiesmal vesicles (Taylor 1987). These thecal plates' number, shape and arrangement are species-specific and generally well conserved. Hence, they can be used as reliable identification criteria for distinguishing numerous armoured dinoflagellates at the species level (Fensome *et al.* 1993; Taylor 1987).

One of them is the genus *Protooperidinium* Bergh which harbours over 280 described thecate marine species (Gómez 2012). Some *Protooperidinium* species possess essential ecological roles, such as forming

algal bloom, serving as a conduit for algal toxins, or even regulating the bloom of other dinoflagellates (Gribble *et al.* 2007). Therefore accurate identification of this dinoflagellate at the species level is crucial, particularly for biodiversity assessments or monitoring. The motile and thecate forms are morphologically identified based on the cell size, cell shape, the presence of apical and/or antapical spines, the displacement of the cingulum, and most importantly, the composition and arrangement pattern of the thecal plates (e.g. Hoppenrath *et al.* 2009; Okolodkov 2008).

During inventorying the marine microalgae in Indonesia, we encountered two dinoflagellate cells representing the first record of *Protooperidinium abei* (Paulsen) Balech in Indonesia. This study aims to morphologically characterize, illustrate, describe, and identify this dinoflagellate species using light microscopy (LM).

2. Materials and Methods

2.1. Sampling Location, Collection and Processing

Samplings were conducted in Tanjung Pasir Beach (TPB; GPS: 6.01 S, 106.8 N), Banten, Indonesia in October 10th 2021 (Figure 1). Seawater sample was collected at the surface layer (ca. 0.5 m deep) using a 20 μm mesh plankton net from the pier

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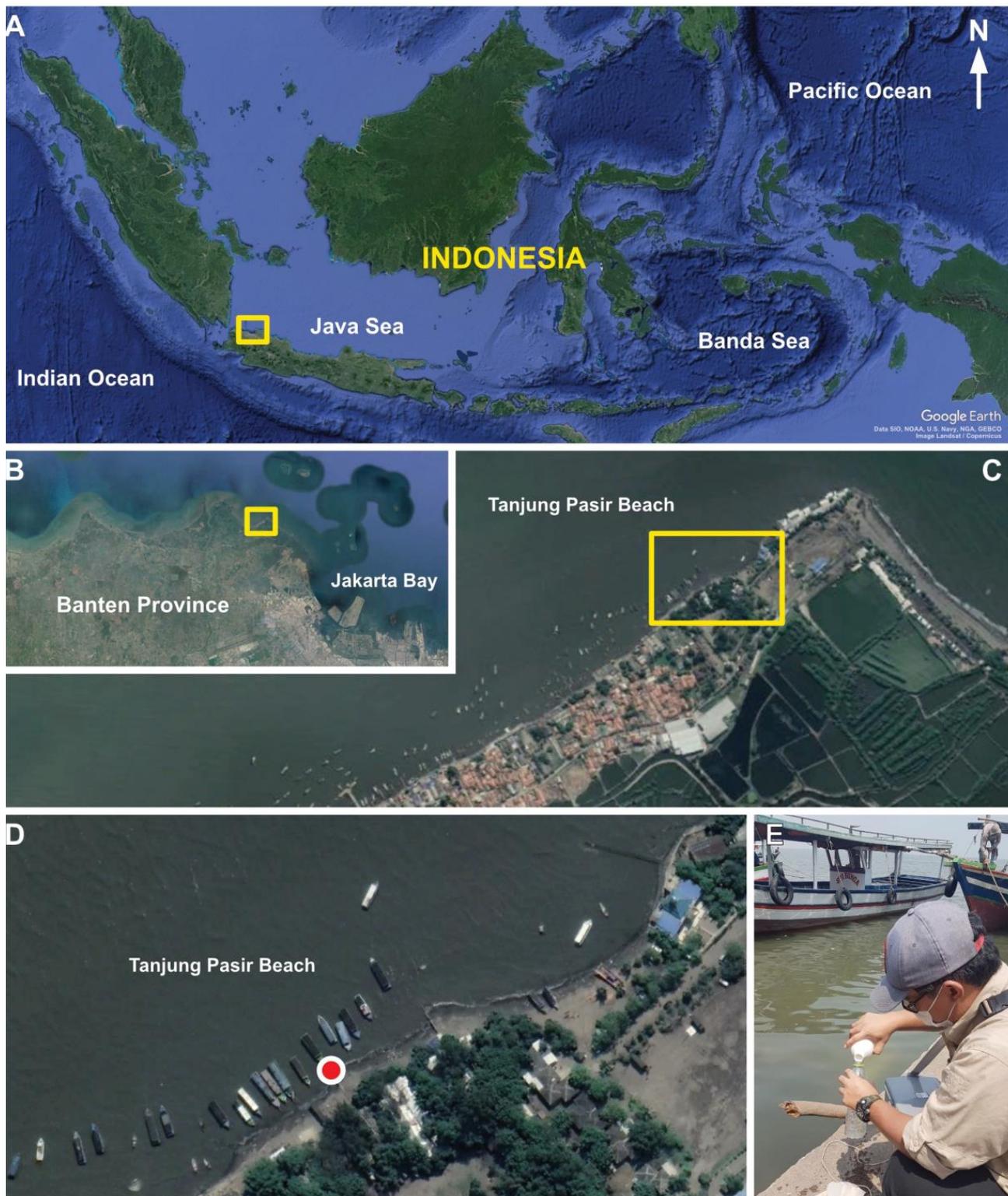


Figure 1. (A) Map of Indonesia indicating the (B-D) sampling location in Tanjung Pasir Beach (TPB), Banten (GPS: 6.01 S, 106.8 N). (E) Seawater sample was collected using a 20 µm mesh-size plankton net from the sampling boat or pier. All satellite images were obtained from Google Earth

and transferred into two 200 ml plastic bottles. The sample was subsequently enriched with a few drops of Daigo's IMK medium (Wako, Tokyo, Japan) before being transported in a cool box to the Laboratory of Algae at the Indonesian Culture Collection (InaCC) in Cibinong, West Java, Indonesia. At the laboratory, samples were immediately transferred into clean plastic Petri dishes and incubated under 25°C with about 30 $\mu\text{mol m}^{-2}\text{s}^{-1}$ fluorescent illumination (12:12 hours light-dark cycles). Two identical dinoflagellate cells were found in the seawater sample. One cell (i.e. TP1a specimen) was isolated using a hand-drawn glass capillary micropipette into one of the 48-well culture plates containing a few drops of IMK medium and incubated under the same conditions mentioned previously. Unfortunately, the TP1a specimen was eventually lost during the culture attempt. Consequently, molecular phylogenetic analyses that require DNA extraction from such microalgal cultures could not be performed. Hence, species-level identification of the dinoflagellate encountered in this study solely relied on the morphological characterization of the other cell (i.e. TP1b specimen) using light microscopy (LM).

2.2. LM Observation, Morphological Characterization, Taxonomic Identification

Light microscopic (LM) observation of the cell (i.e. for general morphology and thecal plates arrangement) was performed using an Olympus CKX 53 inverted microscope (Olympus Corp., Tokyo, Japan). Due to the scarcely available specimens in the sample, we took utmost care when handling the TP1b cell for LM observation and photomicrography. Excess seawater was deliberately siphoned out from the Petri dish using a 2.0 ml plastic pipette to limit the movement area of this specimen until a small pool of seawater containing the TP1b cell remained. A fine hand-drawn glass capillary micropipette was used to carefully adjust the orientation of the cell under the inverted microscope for photomicrography at 20x and 40x objectives magnifications. Acquired micrographs were subsequently post-edited using Adobe Photoshop 21.1.1 (e.g. adjusting the brightness, exposure, contrast, orientation and presenting the cell with clean background). Line drawings of the cell and its thecal plates were manually produced using Affinity Designer ver. 1.10.1 (Serif Europe Ltd).

We adopted the Kofoidan plate tabulation system (Kofoid 1909; Kofoid 1911) to enumerate and determine the thecal plate arrangement pattern of the TP1b specimen. The identity of the species was determined based on general cell morphology and the thecal plate arrangement of *P. abei* originally described by Abé (1927) and supporting reports by Paulsen (1931), Balech (1974), Okolodkov (2008), and Luom *et al.* (2015).

3. Results

3.1. Systematics

Class: Dinophyceae (West and Fritch, 1927)

Order: (Peridinales Haeckel, 1894)

Family: Protoperidinaceae (Balech, 1988)

Genus: *Protoperidinium* (Bergh, 1881)

Protoperidinium abei (Paulsen) (Balech, 1974)

Figures 2-4

Plate tabulation formula: Po, 4', 2a, 7'', 3(?)c, 4s, 5''', 2''''

Locality: Tanjung Pasir Beach, Banten, Indonesia

Basionym: *Peridinium abei* (Paulsen, 1931)

Synonym: *Peridinium biconicum* (Abé, 1927)

3.2. General Cell Morphology

The cells measured 71.97–72.86 μm long and 52.55–52.76 μm ($n = 2$). Cells are fusiform or biconical, with tapered apical and antapical horns (Figures 2A and B). A sharp and pointy spine was present at the antapex (Figure 2B). The apical pore has a slit visible at the ventral and dorsal areas of the apical horn, while two tiny protrusions or processes bordered the left and right margins of the apex (Figures 2C and D). No hyalious or membrane-like structure was observed at the apical pore. The apical horn was bent or curved towards the dorsal area of the cell in lateral view (Figure 2E). The cingulum is median, dividing the epi- and hypotheca almost in the same size, descended leftward, with its left and right distal ends displaced about 1.5x of its width (Figure 2E). The right cingulum end partially covered the ventral area where the flagella were supposedly to emerge (Figure 2F). The anterior and posterior rims of the cingulum were thick, while its furrow was deeply excavated with numerous strong longitudinal ribs parallelly arranged on its wall (Figures 2F and G). The right part of the hypotheca was larger than

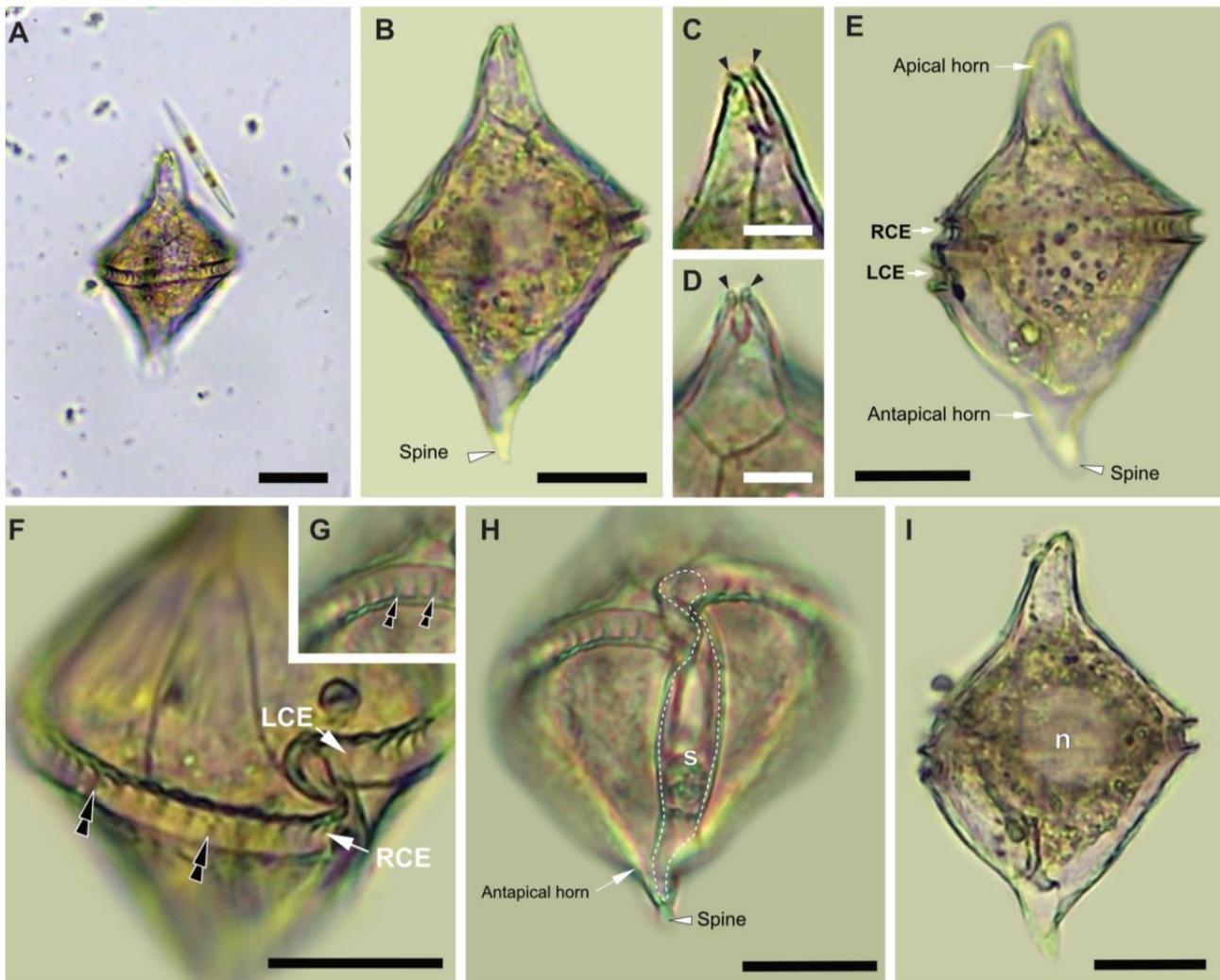


Figure 2. Light micrographs of *P. abei* specimens from TPB, Banten, Indonesia, showing (A) the TP1a specimen isolated for culture attempt. (B–H) TP1b specimen subjected to LM observation showing the (B) general cell shape/outline, the nucleus, and the sharp antapical spine; (C and D), the slit-like apical pore in ventral and dorsal view, respectively (notice the small protrusions at the tip of the apex (black arrowheads)); (E and G) the deeply excavated cingulum furrow with the displaced right (RCE) and left cingulum ends (LCE) (notice the strong longitudinal ribs, also the dorsally-bent apical horn); (H) the narrow sulcus ('s'; area marked with dashed white line), notice the sharp spine at posterior of the antapex; (I) left lateral view showing the median-located nucleus ('n'). Scale bars = 20 μm , except for C–D = 10 μm

the left one, forming the extended antapical horn, tipped with a sharp and pointy spine (Figure 2H). The sulcal area was narrow, excavated and extended towards the posterior part of the antapical horn at the hypotheca (Figure 2H). The nucleus is at the median, just beneath the cingulum girdle (Figure 2I). No chloroplast was observed within the cell, suggesting the heterotrophic nature of this species.

3.3. Thecal Plates Arrangement

The complete thecal plates arrangement of the TP1b specimen is illustrated in Figures 3, 4 and 5A–D. At least 28 thecal plates were enumerated and its

tabulation formula was defined as $\text{Po}, 4', 2a, 7'', 3(?)c, 4s, 5''', 2''''$. The epitheca comprised 14 plates (Figures 3A–H) and comprised one apical pore plate (Po), four apical plates (1'–4'), and two anterior intercalary (1a, 2a), and seven rectangular plates (1''–7''). The 1' plate was 'ortho' and the longest among the epithelial plates (Figure 3A), while the two intercalary plates were hexagonal and similar in size (Figures 3C–E). At the girdle level, three cingular plates were observed (c1–c3) (Figures 3E–H and 3P). The position of the transitional plate was not identified in this study as its border could not be distinguished from the

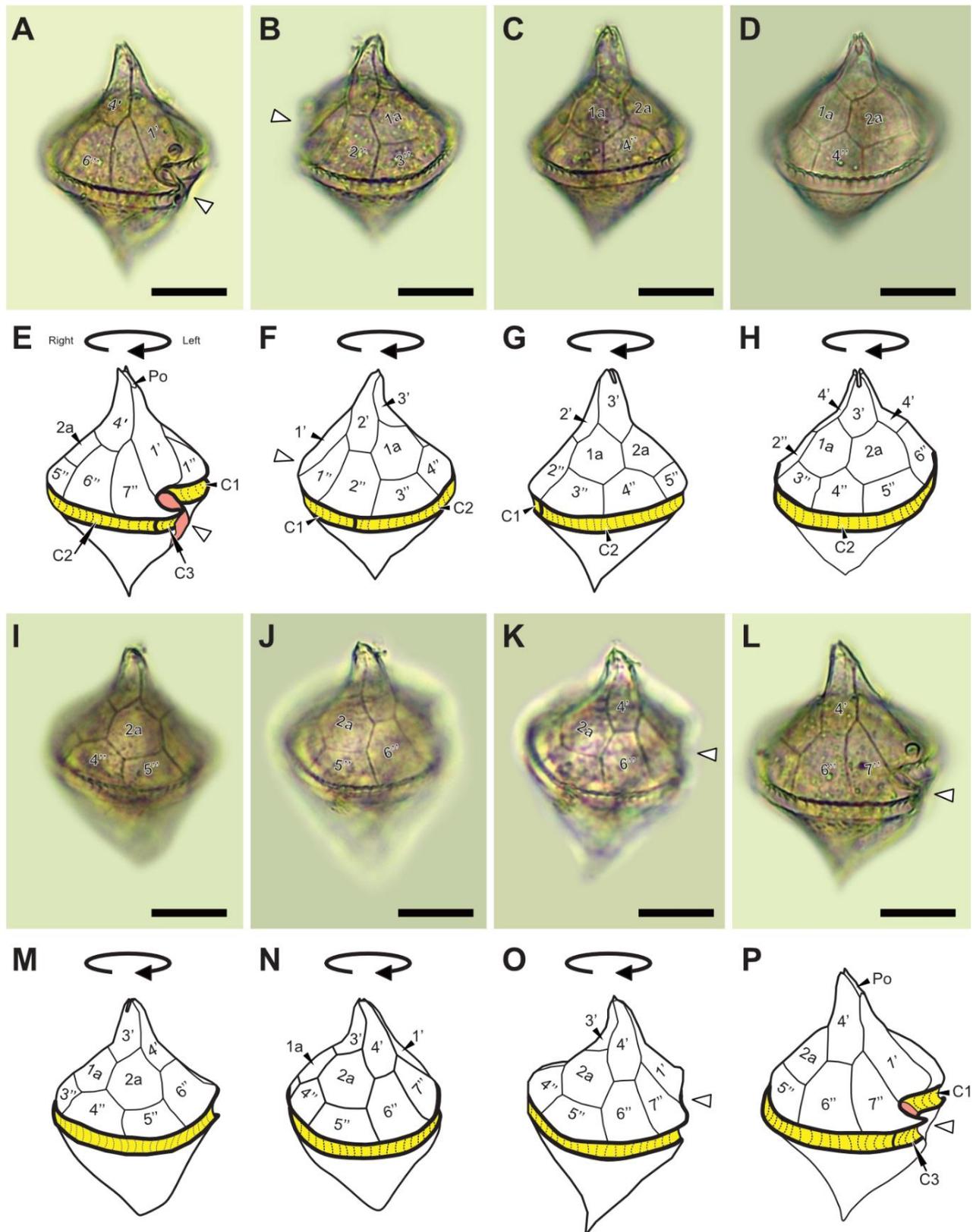


Figure 3. (A-D, I-J) Light micrographs and (E-H, M-P) hand-drawings of *P. abei* (TP1b specimen) showing the epithelial plates arrangement pattern displayed in sequential rightward turning directions. White arrowheads indicate the ventral parts of the cell. Yellow and red indicate the cingulum and sulcus, respectively-scale bars: 20 μ m

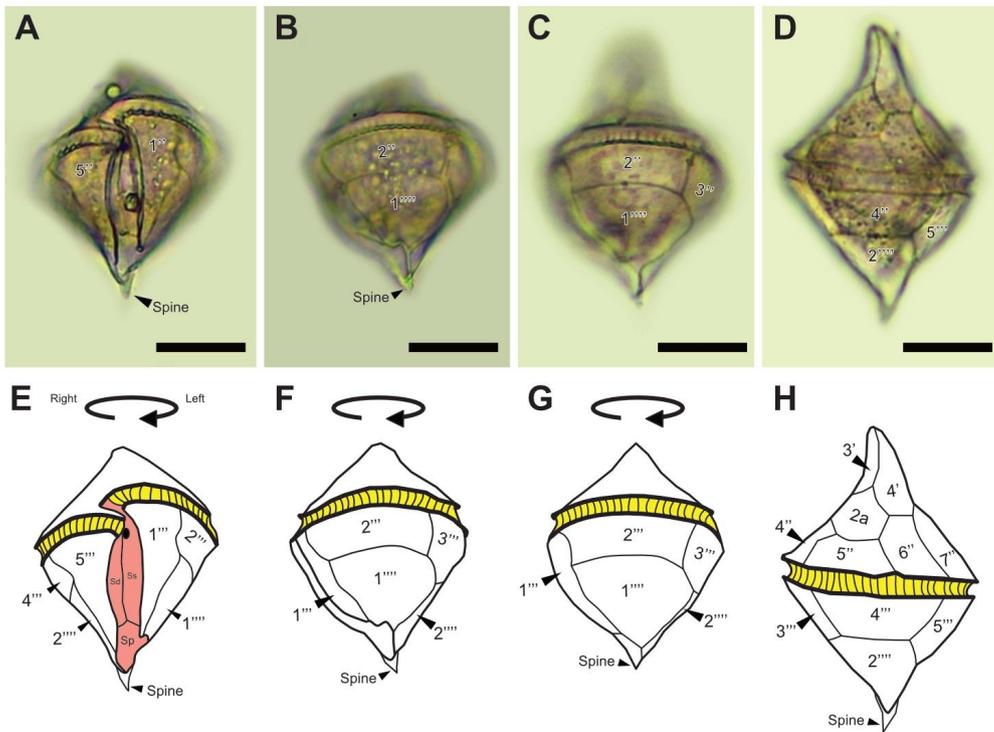


Figure 4. (A-D) Light micrographs and (E-H) line-drawings of *P. abei* (TP1b specimen) showing the sulcal and hypothecal plates arrangements pattern displayed in sequential rightward turning directions. Yellow and red indicate the cingulum and sulcus, respectively-scale bars: 20 μ m

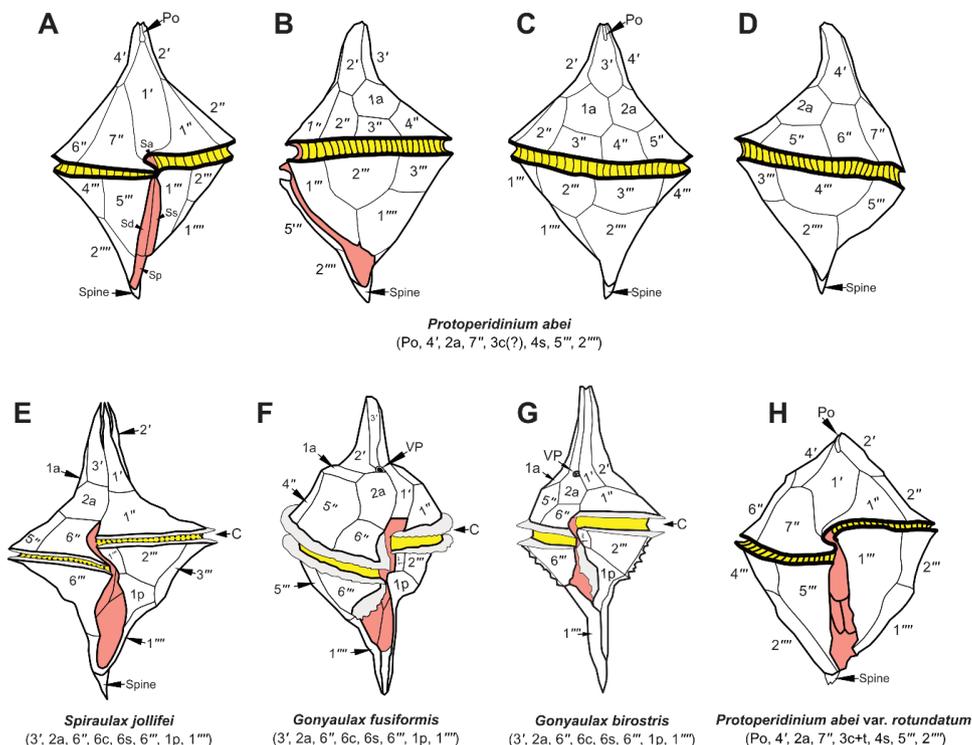


Figure 5. Comparative line drawings show the cell outline and thecal plate arrangement patterns between (A-D) *P. abei* and other dinoflagellate species bearing similar morphology: (E) *Spiraulax jolliffei*, (F) *Gonyaulax fusiformis*, (G) *Gonyaulax birostris*, and (H) *P. abei* var. *rotundatum*. The line drawings of *P. abei* were based on the TP1b specimen observed in this study. The following three species were redrawn based on the report of Carbonell-Moore (1996), while *P. abei* var. *rotundatum* was redrawn based on Omura et al. (2012) with additional information from Luom et al. (2016). Yellow and red colours indicate the cingulum and sulcus, respectively. Images are not to scale

longitudinal ribs of the cingulum at ventral view using LM. Hence, a question mark was added following the '3c' notation to indicate the total unknown number of the cingular plates in our specimen. At the ventral view, the sulcal area of TP1b contained four sulcal plates (Sa, Sd, Ss and Sp) (Figure 3I). Finally, a total of seven hypothecal plates were observed (Figures 3I-L), which consisted of five postcingular plates (1'''-5''') and two antapical plates (1''''-2''').

4. Discussion

Following rigorous LM observation involving the TP1b specimen from TPB, we revealed that the morphology (i.e. cell size, fusiform/biconical shape, the presence of an antapical spine, and cingulum displacement of about 1.5x of its width) combined with the thecal plate tabulation pattern (i.e. Po, 4', 2a, 7'', 3(?)c, 4s, 5''', 2''') of the TP1b specimen undoubtedly conformed to the original description of *P. abei* from Japan (Abé 1927) and other reports of this species (Balech 1974; Okolodkov 2008; Luom *et al.* 2015; Paulsen 1931). Hence, the two identical specimens reported herein were identified as *P. abei*.

The tapered biconical cell shape combined with the lack of two antapical horns in *P. abei* superficially distinguishes this species from the typical and more commonly found *Protoperidinium* spp., like *P. conicum*, *P. obtusum*, *P. oceanicum* and others (e.g. Okolodkov 2008). However, when examined closely, two antapical horns were present at the hypotheca (Figure 2H). Although, the posterior part of the left antapical horn was greatly reduced in size compared to the right one, creating a pseudo-outline as if the cell only has a single antapical horn, especially when viewed laterally. To unfamiliar eyes, this peculiar cell appearance could lead to the misidentification of *P. abei* under LM as other species of dinoflagellate that bear somewhat similar cell outlines, like *Spiraulax jolliffei* (Figure 5E), *Gonyaulax fusiformis* (Figure 5F), or *Gonyaulax birostris* (Figure 5G) (Carbonell-Moore 1996). However, when their thecal plate compositions are taken into account, *P. abei* differs substantially from these planktonic dinoflagellates regarding the overall arrangement pattern of the plates (Figures 5A-G), specifically concerning the presence of an apical pore plate (Po), the number of precingular plates (7'' vs 6''), cingular plates (3-4c vs 6c), sulcal plates (4s vs 6s), and antapical plates (2'' vs 1''). The lack of a posterior intercalary plate (1p) (Figures 5A-D) in *P. abei* further differentiates it from the dinoflagellates above (Figures 5E-G). It signifies the importance of determining the thecal plates tabulation pattern for species-level identification of armoured dinoflagellates.

Our *P. abei* specimens from TPB share similar thecal plate composition and arrangement with *P. abei* var. *rotundata* (Abé) Taylor (Figure 5H). However, our specimens discriminate from the latter species by having more prolonged and tapered apical and antapical horns (Figures 2-4 and 5A-D). *P. abei* var. *rotundata*, on the other hand, possess shorter and somewhat blunt epi- and hypotheca (Figure 5H), also shown by Liu *et al.* (2015), Luom *et al.* (2015), and Luom *et al.* (2016). It is also worth mentioning that a small transitional plate (t) was present in the left ventral part of the cingulum in *P. abei* var. *rotundata* (e.g. Liu *et al.* 2015). Unfortunately, the location of such a plate could not be verified in our study using LM due to the difficulty in differentiating its border with the longitudinal ribs of the cingulum furrow.

Aside from the original description of Abé (1927), the cells of *P. abei* described in this study agree well with the morphology of the specimens reported from other localities, such as the Gulf of Mexico (Okolodkov 2008), Vietnam (Luom *et al.* 2015), and the Red Sea (Prabowo and Agusti 2019). Geographically, *P. abei* has been widely recorded in numerous marine areas, such as Bangladesh (Ahmed *et al.* 2009), Russia (Gail 1950; Kisselev 1950), Black Sea (Zotov 2018), Mediterranean Sea (Gómez 2003), the Caribbean (Merino-Virgilio *et al.* 2013), Colombia (Luzano-Duque *et al.* 2011), Australia (McCarthy 2013) and others (Guiry and Guiry 2018), suggesting its wide distribution, particularly in warm and tropical seas.

In Indonesia, at least 29 *Protoperidinium* species were recorded, of which 28 were identified down to the species level (Table 1). Unfortunately, most of them lack illustrations or morphological descriptions, making it impossible to verify and validate their identity and occurrence in Indonesia accurately. Nevertheless, among the listed *Protoperidinium* species (Table 1), none was *P. abei*, therefore, highlighting the present study as the first to record, illustrate, and describe the morphology of this thecate marine dinoflagellate from Indonesian water. The finding of *P. abei* in Indonesia further extends its geographical distribution to include the equatorial waters of Southeast Asia.

In conclusion, this study successfully identified the two dinoflagellate specimens found in Tanjung Pasir Beach (TPB), Banten as *P. abei* and reported for the first time its occurrence in Indonesia. Although identification of microalgal species based on polyphasic approaches (e.g. combining morphological, molecular, and chemical data) is currently preferred, we demonstrated that species-level identification using LM is still highly relevant for dinoflagellates, particularly thecate marine species.

Table 1. Recorded *Protoperidinium* species in Indonesia

| Species | Reference |
|--|--|
| <i>Protoperidinium abei</i> | This study |
| <i>Protoperidinium avellana</i> | Rukmanasari and Thahir (2020) |
| <i>Protoperidinium balticum</i> | Rachman (2020) |
| <i>Protoperidinium cf. americanum</i> | Rukmanasari and Thahir (2020) |
| <i>Protoperidinium cf. divergen</i> | Rukmanasari and Thahir (2020) |
| <i>Protoperidinium cf. excentricum</i> | Rukmanasari and Thahir (2020) |
| <i>Protoperidinium claudicans</i> | Rukmanasari and Thahir (2020), Furio <i>et al.</i> (2012) |
| <i>Protoperidinium compressum</i> | Furio <i>et al.</i> (2012) |
| <i>Protoperidinium conicoides</i> | Rukmanasari and Thahir (2020) |
| <i>Protoperidinium conicum</i> | Furio <i>et al.</i> (2012), Sidharta and Ahyadi (2007) |
| <i>Protoperidinium curtipes</i> | Rachman (2020) |
| <i>Protoperidinium denticulatum</i> | Furio <i>et al.</i> (2012) |
| <i>Protoperidinium depressum</i> | Rachman (2020) |
| <i>Protoperidinium divergens</i> | Rachman (2020), Sidharta and Ahyadi (2007), Lestari <i>et al.</i> (2021) |
| <i>Protoperidinium faltipes</i> | Rachman (2020) |
| <i>Protoperidinium fukuyoi</i> | Rukmanasari and Thahir (2020) |
| <i>Protoperidinium leonis</i> | Furio <i>et al.</i> (2012), Sidharta and Ahyadi (2007) |
| <i>Protoperidinium minutum</i> | Rachman (2020) |
| <i>Protoperidinium nudum</i> | Likumahuwa <i>et al.</i> (2021) |
| <i>Protoperidinium oblongum</i> | Rukmanasari and Thahir (2020); Furio <i>et al.</i> (2012) |
| <i>Protoperidinium oceanicum</i> | Rachman (2020); Thoah <i>et al.</i> (2010) |
| <i>Protoperidinium pentagonum</i> | Rachman (2020); Rukmanasari and Thahir (2020); Furio <i>et al.</i> (2012) |
| <i>Protoperidinium punctulatum</i> | Rukmanasari and Thahir (2020) |
| <i>Protoperidinium rectum</i> | Rachman (2020) |
| <i>Protoperidinium roseum</i> | Rachman (2020) |
| <i>Protoperidinium sphaericum</i> | Rachman (2020) |
| <i>Protoperidinium subinerme</i> | Furio <i>et al.</i> (2012) |
| <i>Protoperidinium subinerum</i> | Rukmanasari and Thahir (2020) |
| <i>Protoperidinium pellucidum</i> | Sidharta and Ahyadi (2007) |
| <i>Protoperidinium</i> spp. | Thoah <i>et al.</i> (2010); Furio <i>et al.</i> (2012); Syafriani dan Afriadi (2018); Mujib <i>et al.</i> (2015); Thoah and Rachman (2012); Lestari <i>et al.</i> 2021; Pello <i>et al.</i> (2017); Thoah <i>et al.</i> (2019) |

Therefore, we encourage future biodiversity studies of dinoflagellates in Indonesia to harness the full potential of LM for supplying each reported species with high-quality photomicrographs for taxonomic verification and validation instead of presenting an inventory checklist of the encountered taxa.

Acknowledgements

This study was partially supported by Kurita Water and Environment Foundation (KWEF) through the Kurita Overseas Research Grant (KORG) 2021 (Ref. No. 21Pid012-7K) awarded to DAP.

References

- Abé, T.H., 1927. Report of the biological survey of Mutsu Bay. 3. Notes on the protozoan fauna of Mutsu Bay. I. *Peridinales*. *Sci. Rep. Tohoku Imp. Univ. Ser. 4*, 383-438.
- Ahmed, Z.U., Khondker, M., Begum, Z.N.T., Hassan, M.A., Kabir, S.M.H., Ahmad, M., 2009. ALGAE, charophyta-rhodophyta. In: Ahmed, ZU (Eds.), *Encyclopedia of Flora and Fauna of Bangladesh Vol. 4*. Dhaka: Asiatic Society of Bangladesh. pp. 544.

- Balech, E., 1974. El genero "*Protoperidinium*" Bergh, 1881 ("Peridinium" Ehrenberg 1831, partim). *Revta Arg. Cienc. Nat. "B. Rivadavia" Hidrobiol.* 4, 1-79.
- Carbonell-Moore, M.C., 1996. On *Spiraulax jolliffei* (Murray et Whitting) Kofoid and *Gonyaulax fusiformis* Graham (Dinophyceae). *Bot. Mar.* 39, 347-370. <https://doi.org/10.1515/botm.1996.39.1-6.347>
- Fensome R.A., Taylor F.J.R., Norris G., Sarjeant W.A.S., Wharton D.I., Williams G.L., 1993. A Classification of Living and Fossil Dinoflagellates. American Museum of Natural History, New York.
- Furio, E.F., Azanza, R.V., Fukuyo, Y., Matsuoka, K., 2012. Review of geographical distribution of dinoflagellate cysts in Southeast Asian coasts. *Coast. Mar. Sci.* 35, 20-33.
- Gail, G.I., 1950. Opredelitel' fitoplanktona Yaponskogo morya (Manual for identification of the phytoplankton of the Sea of Japan). *Izvestiya Tikhookeanskogo Nauchno-issledovatel'skogo Instituta Rybnogo Khozyaystva.* 3, 1-177.
- Gómez, F., 2003. Checklist of Mediterranean free-living dinoflagellates. *Bot. Mar.* 46, 215-242. <https://doi.org/10.1515/BOT.2003.021>
- Gómez, F., 2012. A checklist and classification of living dinoflagellates (Dinoflagellata, Alveolata). *Cicmar Oceanides.* 27, 65-140. <https://doi.org/10.37543/oceanides.v27i1.111>
- Guiry, M.D., Guiry, G.M., 2018 AlgaeBase: *Protoperidinium abei* (Paulsen) Balech 1974. Available at: https://www.algaebase.org/search/species/detail/?species_id=70914. [Date accessed: 13 March 2022]

- Gribble, K.E., Nolan, G., Anderson, D.M., 2007. Biodiversity, biogeography and potential trophic impact of *Protooperidinium* spp. (Dinophyceae) off the southwestern coast of Ireland. *J. Plankton Res.* 29, 931–947. <https://doi.org/10.1093/plankt/fbm070>
- Hackett, J.D., Anderson, D.M., Erdner, D.L., Bhattacharya, D., 2004. Dinoflagellates: a remarkable evolutionary experiment. *Am. J. Bot.* 91, 1523–1534. <https://doi.org/10.3732/ajb.91.10.1523>
- Hoppenrath, M., Elbrächter, M., Drebes, G., 2009. *Marine Phytoplankton: Selected Microphytoplankton Species from the North Sea around Helgoland and Sylt. Kleine Senckenberg-Reihe*, 49. E. Schweizerbart Science Publisher, Stuttgart.
- Kisselev, I.A., 1950. *Armoured Flagellates (Dinoflagellate) from the Seas and Freshwaters of the USSR (in Russian)*. USSR Academic and Scientific Publishing, Moscow-Leningrad.
- Kofoid, C.A., 1909. On *Peridinium steinii* Jörgensen, with a note on the nomenclature of the skeleton of the Peridinidae. *Archiv für Protistenkunde*. 16, 25–47.
- Kofoid, C.A., 1911. *Dinoflagellata of the San Diego Region, IV: the Genus Gonyaulax, with Notes on its Skeletal Morphology, and a Discussion of its Generic and Specific Characters*. University of California Publishing Service, Berkeley.
- Le Bescot, N., Mahé, F., Audic, S., Dimier, C., Garet, M.J., Poulain, J., Wincker, P., de Vargas, C., Siano, R., 2016. Global patterns of pelagic dinoflagellate diversity across protist size classes unveiled by metabarcoding. *Environ. Microbiol. Rep.* 18, 609–626. <https://doi.org/10.1111/1462-2920.13039>
- Lestari, H.A., Samawi, M.F., Faizal, A., Moore, A.M., Jompa, J., 2021. Diversity and abundance of phytoplankton in the Coastal Waters of South Sulawesi. *HAYATI Journal of Biosciences*. 28, 199–211. <https://doi.org/10.4308/hjb.28.3.199>
- Likumahua, S., Sangiorgi, F., de Boer, M.K., Tatipatta, W.M., Pelasula, D.D., Polnaya, D., Hehuwat, J., Siahaya, D.M., Buma, A.G.J., 2021. Dinoflagellate cyst distribution in surface sediments of Ambon Bay (eastern Indonesia): Environmental conditions and harmful blooms. *Mar. Pol. Bul.* 166, 112269. <https://doi.org/10.1016/j.marpolbul.2021.112269>
- Liu, T., Mertens, K.N., Ribeiro, S., Ellegaard, M., Matsuoka, K., Gu, H., 2015. Cyst-theca relationships and phylogenetic positions of *Peridiniales* (Dinophyceae) with two anterior intercalary plates, with description of *Archaeperidinium bailongense* sp. nov. and *Protooperidinium fuzhouense* sp. nov. *Phycol. Res.* 63, 134–151. <https://doi.org/10.1111/pre.12081>
- Luom, P.T., Lam, N.N., Hai, D.N., 2015. Taxonomy of the genus *Protooperidinium* (Dinoflagellate) species in the Vietnamese Waters. Subgenus *Archaeperidinium*. In: *Poster presented at the international workshop on developing life-supporting marine ecosystems along with Asia-Pacific coasts—a synthesis of physical and biological data for the science-based management and socio-ecological policy making*. Nha Trang, 21–23 December 2015.
- Luom, P.T., Lam, N.N., Hai, D.N., 2016. Taxonomy of dinoflagellates, the genus *Protooperidinium* (*Archaeperidinium*), in coastal waters of Vietnam. *Academia Journal of Biology*. 38, 39–52. <https://doi.org/10.15625/0866-7160/v38n1.7596>
- Lozano-Duque, Y., Vidal, L.A., Navas S.G.R., 2011. Lista de especies de dinoflagelados (Dinophyta) registrados en el mar Caribe Colombiano. *Boletín de Investigaciones Marinas y Costeras*. 40, 10–30. <https://doi.org/10.25268/bimc.invemmar.2011.40.2.116>
- McCarthy, P.M., 2013. Census of Australian Marine Dinoflagellates. Australian Biological Resources Study, Canberra. Available at: http://www.anbg.gov.au/abrs/Dinoflagellates/index_Dino.html. [Date accessed: 1 April 2022]
- Merino-Virgilio, F. del C., Okolodkov, Y.B., Aguilar-Trujillo, A.C., Herrera-Silveira, J.A., 2013. Phytoplankton of the northern coastal and shelf waters of the Yucatan Peninsula, southeastern Gulf of Mexico, Mexico. *Check List*. 9, 771–779. <https://doi.org/10.15560/9.4.771>
- Mujib, A.S., Damar, A., Wardiatno, Y., 2015. Distribusi spasial dinoflagellata planktonik di perairan Makasar, Sulawesi Selatan. *Jurnal Ilmu dan Teknologi Kelautan Tropis*. 7, 479–492. <https://doi.org/10.29244/jitkt.v7i2.11033>
- Okolodkov, Y., 2008. *Protooperidinium* Bergh (Dinophyceae) of the National Park Sistema Arrecifal Veracruzano, Gulf of Mexico, with a key for identification. *Acta Bot. Mex.* 84, 93–149. <https://doi.org/10.21829/abm84.2008.1068>
- Paulsen, O., 1931. Études sur le microplancton de la mer d'Alboran. *Trabajos Instituto Español de Oceanografía*. 4, 1–104.
- Omura, T., Iwataki, M., Borja, V.M., Takayama, H., Fukuyo, W., 2012. *Fitoplankton Laut Pasifik Barat*. Perusahaan Kouseisha Kouseikaku, Tokyo.
- Pello, F.S., Haumahu, S., Huliselan, N.V., Tuapattinaja, M.A., 2017. Cyst accumulation in the bottom sediments in Inner Ambon Bay and Kao Bay, Indonesia. *AAAL Bioflux*. 10, 1–7.
- Prabowo, D.A., Agusti, S., 2019. Free-living dinoflagellates of the central Red Sea, Saudi Arabia: variability, new records and potentially harmful species. *Mar. Pol. Bul.* 141, 629–648. <https://doi.org/10.1016/j.marpolbul.2019.03.012>
- Rachman, A., 2020. Checklist and estimation of total number of phytoplankton species in Pari, Tidung, and Payung Islands, Indonesia. *Biodiversitas Journal of Biological Diversity*. 21, 2446–2458. <https://doi.org/10.13057/biodiv/d210616>
- Rukminasari, N., Tahir, A., 2020. Species assemblages and distribution of dinoflagellate cysts from three estuaries sediments of Makassar Strait, Eastern Indonesia. *Online Journal of Biological Sciences*. 21, 232–244. <https://doi.org/10.3844/ojbsci.2021.232.244>
- Sidharta, B.R., Ahyadi, H., 2007. Possible occurrence of toxic and harmful phytoplankton in Lembar Bay, Lombok, Indonesia. *Mar. Res. Indonesia*. 32, 197–202. <https://doi.org/10.14203/mri.v32i2.455>
- Syafriani, R., Apriadi, T., 2018. Keanekaragaman fitoplankton di perairan estuari sei terusan, kota tanjungpinang. *Limnotek: Perairan Darat Tropis di Indonesia*. 24, 74–82.
- Taylor, F.J.R., 1987. Dinoflagellate morphology. In: Taylor, F.J.R. (Eds.), *The Biology of Dinoflagellates (Bot. Monographs, 21)*. Oxford: Blackwell Scientific publications, pp. 24–91.
- Taylor, F.J.R., Hoppenrath, M., Saldarriaga, J.F., 2008. Dinoflagellate diversity and distribution. *Biodivers. Conserv.* 17, 407–418. <https://doi.org/10.1007/s10531-007-9258-3>
- Toha, H., Adnan, Q., Sidabutar, T., 2010. Note on the occurrence of phytoplankton and its relation with mass mortality in the Jakarta Bay, May and November 2004. *Makara Journal of Science*. 2, 63–67. <https://doi.org/10.7454/mss.v11i2.258>
- Toha, H., Rachman, A., 2012. Temporal variation in *Ceratium* spp. abundance recorded in Jakarta Bay. *Mar. Res. Indonesia*. 37, 35–45. <https://doi.org/10.14203/mri.v37i1.35>
- Toha, H., Bayu, M.D., Rachman, A., Senming, T., 2019. Phytoplankton community in the Lembeh Strait, Bitung and Wori Beach, Manado, North of Sulawesi, Indonesia. *Majalah Ilmiah Biologi BIOSFERA: A Scientific Journal*. 36, 118–125.
- Zotov, A.B., 2018. Unification of calculation the volume of alga for phytoplankton of the Black Sea to the standards of the EU Marine Strategy. *Algologia*. 28, 208–232. <https://doi.org/10.15407/alg28.02.208>