

Further observations on a hypothecal pore in the genus *Protoperidinium* Bergh (Dinoflagellata)

Observaciones adicionales del poro hipotecal en el género *Protoperidinium* Bergh (Dinoflagellata)

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ABSTRACT

The data on 21 *Protoperidinium* species (including 8 species assigned to the genus *Peridinium*, which supposedly also belong to the genus *Protoperidinium*) with a hypothecal pore on the first postcingular plate are summarized. The hypothecal pore is shown to be present not only in the species with the first apical plate of the *para*-type, but also in some species with the *meta*-type. It is confirmed that the pore is almost exclusively associated with the *hexa* second intercalary plate. The pore is thought to be present in closely related species and to be a reliable diagnostic feature to differentiate *Protoperidinium* species. At least five groups of morphologically similar and supposedly related taxa can be distinguished: (1) *Protoperidinium affine*, *P. pallidum* and *P. pellucidum*; (2) *P. curvipes* and *P. variegatum*; (3) *P. diabolium* and *P. dodgei*; (4) *P. cruciferum*, *P. cf. cruciferum*, *Protoperidinium* sp. 1 (*meta-hexa*) and *Peridinium acutum*; (5) *P. ovum* and *Protoperidinium* sp. 2 (*para-penta*).

Key words: Dinoflagellates, hypothecal pore, *Protoperidinium*, thecal morphology.

RESUMEN

Se presentan los datos resumidos de 21 especies de *Protoperidinium* (incluyendo 8 especies asignadas al género *Peridinium*, las cuales supuestamente también pertenecen al género *Protoperidinium*) con un poro hipotecal en la primera placa postcingular. El poro hipotecal se encuentra presente no sólo en las especies con la primera placa apical del tipo *para*, sino también en algunas especies con el tipo *meta*. Esto confirma que el poro está casi exclusivamente asociado siempre con la segunda placa intercalar *hexa*. El poro, sin embargo, puede presentarse en especies cercanamente relacionadas y es una característica diagnóstica confiable para diferenciar especies de *Protoperidinium*. Al menos cinco grupos, morfológicamente similares y taxa supuestamente relacionados, pueden ser distinguidos: (1) *Protoperidinium affine*, *P. pallidum* y *P. pellucidum*; (2) *P. curvipes* y *P. variegatum*; (3) *P. diabolium* y *P. dodgei*; (4) *P. cruciferum*, *P. cf. cruciferum*, *Protoperidinium* sp. 1 (*meta-hexa*) y *Peridinium acutum*; (5) *P. ovum* y *Protoperidinium* sp. 2 (*para-penta*).

Palabras clave: Dinoflagelados, poro hipotecal, *Protoperidinium*, morfología tecal.

INTRODUCTION

A hypothecal pore is a peculiar structure in the first postcingular plate (1'') in some species of the genus *Protoperidinium* Bergh. It was first described in *P. cruciferum* Balech by Balech (1971a). In this species, the hypothecal pore is formed by four big dots forming a cross or by three dots (Balech, 1971a, 1973, 1974, 1988). In other species in which the hypothecal pore has been found, the pore looks like an opening on the first postcingular plate. The first species with the hypothecal pore as an opening, *P. diabolus* (Cleve) Balech, was described by Balech (1976a). The presence of the hypothecal pore allowed Balech (1988) to describe a new subspecies, *P. pellucidum* Bergh subsp. *stellatum* Balech. Abé (1981) reported the presence of the hypothecal pore under the name "ventral pore" in nine species ascribed to the group *Paraperidinium* of the section *Pellucida*. Dodge (1987) revised the results obtained by Balech and Abé, finding the hypothecal pore in eight species, of which he identified seven. To avoid the confusion with the ventral pore characteristic of some species of the genera *Alexandrium* Halim and *Gonyaulax* Diesing, which is located on the first apical plate (1'), Dodge offered the term "hypothecal pore". With the use of the scanning electron microscopy, he showed that the hypothecal pore consists of 9-16 small perforations of about 0.1 µm diameter. Also, he stressed that all species possessing the hypothecal pore have a six-sided, or the *para* type, first apical plate. Besides, the hypothecal pore was described in a new species from the NE Atlantic, *P. dodgei*, which is morphologically similar to *P. diabolus* and *P. longipes* (Karsten) Balech, and was reported for *P. affine* and *P. variegatum* (Peters) Balech (Okolodkov, 1997, 2002).

In this paper, new data on other *Protoperidinium* species, which have the hypothecal pore are presented, and the data on all species of the genera *Protoperidinium* and *Peridinium* (also supposedly belonging to the genus *Protoperidinium*) possessing the pore are summarized.

MATERIAL AND METHODS

Samples in which the thecal morphology of *Protoperidinium* species was studied came from the Eurasian Arctic (1980-1997), the Ross Sea (1998), the NE Atlantic (1988-1990), the Mexican Pacific (2000) and the Gulf of Mexico (1983). The material was collected by a plankton net, mesh 20 µm or 70 µm, and fixed with 2-4% formalin. To examine the thecal morphology in detail, Trypan Blue was added to water mounts (Lebour, 1925). The following number of cells has been studied in detail: *Protoperidinium* sp. 1 (*meta-hexa*) – 10, *Protoperidinium* sp. 2 (*para-hexa*) – 7, *P. dodgei* Okolodkov – 3, *P. pallidum* (Ostenfeld) Balech – 5, *P. pellucidum* – 7, *P. affine*

(Balech) Balech – 30, *P. variegatum* (Peters) Balech – 15. A Zeiss Photomicroscope supplied with the objectives 10/0.22, 16/0.35, 25/0.45, Ph2 40/0.65 and the phase contrast was used in combination with a Sony color digital video camera ExwaveHAD and the program KS 300, version 3.0, Carl Zeiss Vision GmbH. The maximum magnification under which the cells were studied under the microscope reached 800. Measurements of the hypothecal pore size were performed in digital images based on the cell length and width measured during microscope observations.

RESULTS AND DISCUSSION

Among 23 studied endemic Antarctic *Protoperidinium* species, only 2 of them were found to have the hypothecal pore, *P. affine* and *P. variegatum* (Okolodkov, 2002). Although the Antarctic *Protoperidinium* species were studied in much detail by Balech (1957, 1958, 1962, 1968, 1976b), it seems that he overlooked the hypothecal pore in these two species. Another four species with the hypothecal pore were found in the Mexican Pacific and the Gulf of Mexico (Table 1). The taxa assigned to the genus *Peridinium* Ehrenberg described by different authors, most likely, belong to the genus *Protoperidinium* which is predominant in the marine environment (Table 2). Although Balech (1994) discusses the synonymy of *Peridinium brachypus* Abé, *P. parvum* Abé and *P. rhomboidale* Abé mentioned in table 2, he does not propose any nomenclatural changes. According to him, *P. brachypus* "es especie muy difícilmente separable de *Protoperidinium capurro*" (Balech, 1994: 63), "homónimo posterior y, probablemente = *P. capurro*" (Balech, 1994: 78); *Peridinium parvum* "parece ser mi *P. cruciferum*" (Balech, 1994: 64) and it is "casi seguro" synonymous to *Protoperidinium cruciferum* (Balech, 1994: 79); *Peridinium rhomboidale* "corresponde a mi *Protoperidinium pallidum daedalum* y *P. cerasiformis*" (Balech, 1994: 64). Besides, the problem is that to transfer the discussed *Peridinium* into the genus *Protoperidinium*, one should be sure that these *Peridinium* species have a certain number of the cingular plates – the main diagnostic feature, which distinguishes the two genera. The original drawings and descriptions of the *Peridinium* species included into table 2 do not permit us to make comparison. Thus, based on the general external morphology of the theca, we can only suggest that all *Peridinium* species mentioned in table 2 belong to the genus *Protoperidinium*.

Most species with the hypothecal pore have the 1' plate of the *para* type, although six species with the *meta* first apical plate were observed. Thus, it seems unlikely that the hypothecal pore is exclusively or nearly exclusively associated with the *para* type, as was emphasized by Dodge (1987).

Table 1. *Protopteridinium* species reported with the hypothecal pore

Species	1' plate	2a plate	Antapical spines	References
<i>P. affine</i> (Balech) Balech	<i>para</i>	<i>hexa</i>	short	Dodge, 1987; Okolodkov, 2002, present study (Fig. 1a-d, 10, 11)
<i>P. cruciferum</i> Balech	<i>meta</i>	<i>hexa</i>	short	Balech, 1971a, 1973, 1974, 1988
<i>P. curvipes</i> (Ostenfeld) Balech	<i>meta</i> or <i>para</i>	<i>neutra</i> , <i>quadra</i> , <i>penta</i> or <i>hexa</i>	short	Dodge, 1987
<i>P. diabolium</i> (Cleve) Balech	<i>para</i>	<i>hexa</i>	long	Balech, 1976a; Dodge, 1987
<i>P. dodgei</i> Okolodkov	<i>para</i>	<i>hexa</i>	long	Okolodkov, 1997; present study (Fig. 2a-d)
<i>P. ovum</i> (Schiller) Balech	<i>para</i>	<i>hexa</i>	medium	Dodge, 1987; present study (Fig. 3, 12)
<i>P. pallidum</i> (Ostenfeld) Balech	<i>para</i>	<i>hexa</i>	medium	Abé, 1981; Dodge, 1987; present study (Fig. 4, 13)
<i>P. pellucidum</i> Bergh	<i>para</i>	<i>hexa</i>	medium	Abé, 1981; Dodge, 1987; Balech, 1988 (subsp. <i>stellatum</i> Balech); present study (Fig. 5, 14)
<i>P. cf. cruciferum</i> Balech	<i>meta</i>	<i>hexa</i>	short	present study (Fig. 6a, b)
<i>Protopteridinium</i> sp. 1	<i>meta</i>	<i>hexa</i>	no spines	present study (Fig. 7a-c, 15, 16)
<i>Protopteridinium</i> sp. 2	<i>para</i>	<i>hexa</i>	short	present study (Fig. 8a, b, 17, 18)
<i>P. variegatum</i> (Peters) Balech	<i>para</i>	<i>hexa</i> or <i>penta</i>	short	Okolodkov, 2002, present study (Fig. 9a, b, 19-21)

Rather, the hypothecal pore is almost exclusively associated with the *hexa* second intercalary plate (Tables 1 and 2). Within the *Protopteridinium* and *Peridinium* species with the hypothecal pore, at least five groups of morphologically similar and supposedly related taxa can be distinguished: (1) Species with the *para* 1' plate, the *hexa* 2a plate and short or

medium antapical spines, cells are usually slightly longer than wide - *Protopteridinium affine*, *P. pallidum* and *P. pellucidum*; (2) Species with the *para* or *meta* 1' plate, variable 2a plate, and short antapical spines, cells are slightly compressed apically-antapically - *P. curvipes* (Ostenfeld) Balech and *P. variegatum*; (3) Species with the *para* 1' plate, the *hexa* 2a plate and long antapical spines, cells are usually noticeably longer than wide - *P. diabolium* and *P. dodgei*; (4) Species with the *meta* 1' plate and *hexa* 2a plate and short antapical spines, cells are slightly wider than long - *P. cruciferum*, *P. cf. cruciferum*, *Protopteridinium* sp. 1 (*meta-hexa*) and *Peridinium acutum* (Fauré-Frémiet) Fauré-Frémiet ex Abé; (5) Species with the *para* 1' plate, the *hexa* 2a plate and one or two short or medium antapical spines and a prominent sulcal list formed by the right sulcal (Sp) plate, cells are slightly longer than wide - *P. ovum* (Schiller) Balech and *Protopteridinium* sp. 2 (*para-hexa*). The latter is morphologically similar to *P. ovum*, however, it has only one (right) antapical spine, more displaced cingulum (usually about one-width of the cingulum), more rounded cell shape, smaller size and the hypothecal pore located closer to the cingulum. The 1' and 2a plates are similar in these two species. In general, the features described above allow to ascribe our *Protopteridinium* sp. 2 (*para-hexa*) to the species designated by Balech (1988: 122, pl. 52, fig. 13-15) as *Protopteridinium* sp. K, although it is also very similar to *P. capurroi* (Balech) Balech subsp. *subpellu-*

Table 2. *Peridinium* species (supposedly belonging to the genus *Protopteridinium*) reported with the hypothecal pore

Species	1' plate	2a plate	Antapical spines	References
<i>P. acutum</i> (Fauré-Frémiet)	<i>meta</i>			
Fauré-Frémiet ex Abé	or <i>para</i>	<i>hexa</i>	medium	Abé, 1981
<i>P. brachypus</i> Abé	<i>para</i>	<i>hexa</i>	short	Abé, 1981
<i>P. globosum</i> (Gourret) Abé	<i>para</i>	<i>hexa</i>	long	Abé, 1981
<i>P. parvum</i> Abé	<i>meta</i>	<i>hexa</i>	short	Abé, 1981
<i>P. rhomboidale</i> Abé	<i>para</i>	<i>hexa</i>	short	Abé, 1981
<i>P. schilleri</i> Paulsen				
var. <i>complexum</i> Abé	<i>para</i>	<i>hexa</i>	medium	Abé, 1981
<i>P. spinosum</i> Schiller				
(as <i>P. spinulosum</i> , by mistake)	<i>para</i>	<i>hexa</i>	medium	Abé, 1981
<i>Peridinium</i> sp.	no data	no data	no data	Dodge, 1987

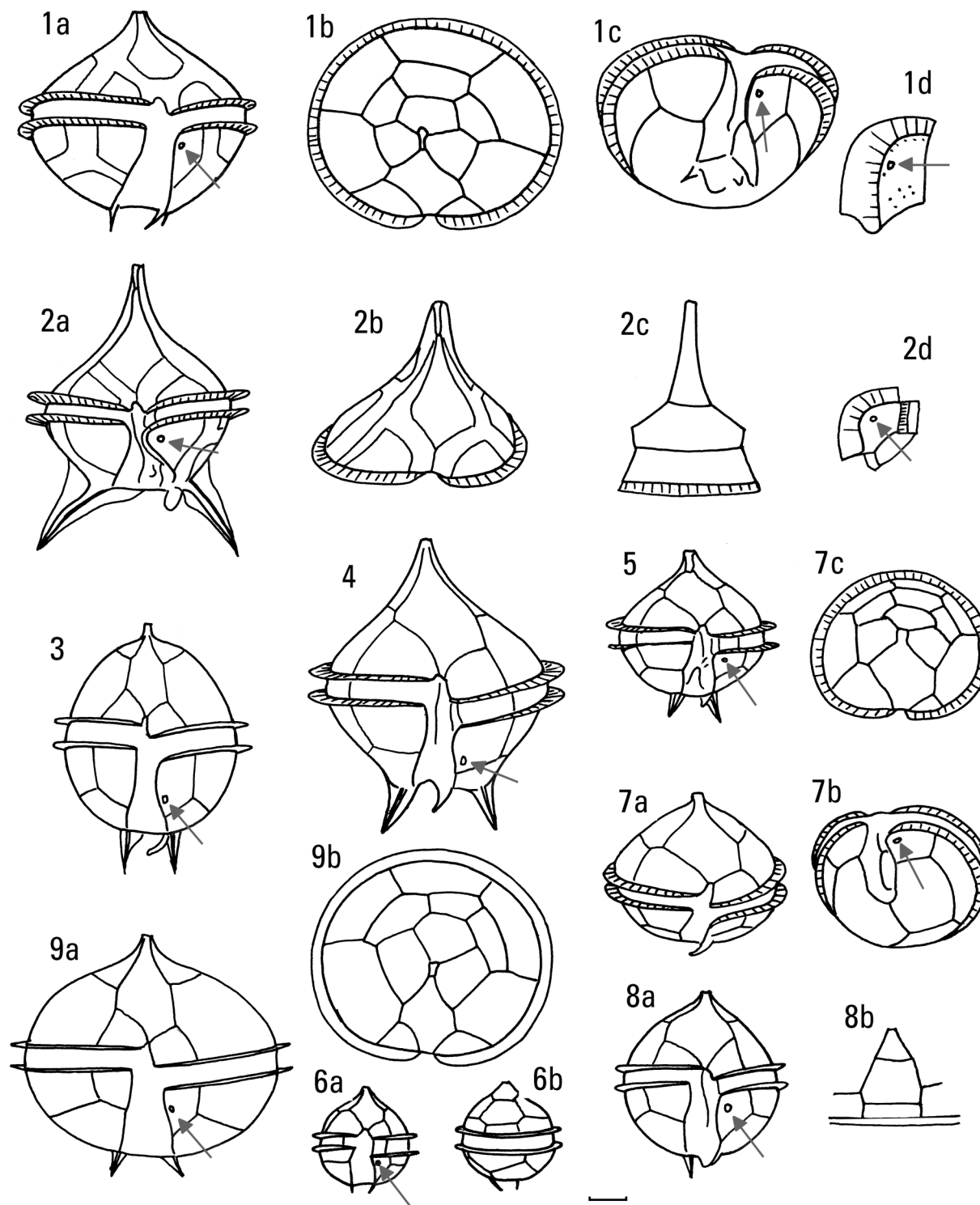


Fig. 1. *Protoperidinium affine*, Ross Sea: a – ventral view; b – apical view; c – ventral-antapical view; d – first postcingular plate (1^{'''}). Fig. 2. *Protoperidinium dodgei*, NE Atlantic (redrawn from Okolodkov, 1997): a – ventral view; b – ventral view (epitheca); c – dorsal plates of epitheca; d – first postcingular plate (1^{'''}). Fig. 3. *Protoperidinium ovum*, Gulf of Mexico, ventral view. Fig. 4. *Protoperidinium pallidum*, SE Mexican Pacific, ventral view. Fig. 5. *Protoperidinium pellucidum*, NW Mexican Pacific, ventral view. Fig. 6. *Protoperidinium* cf. *cruciferum*, SE Mexican Pacific: a – ventral view; b – dorsal view. Fig. 7. *Protoperidinium* sp. 1 (meta-para), Gulf of Mexico: a – ventral view; b – ventral-apical view; c – apical view. Fig. 8. *Protoperidinium* sp. 2 (hexa-para), Gulf of Mexico: a – ventral view; b – dorsal plates of epitheca. Fig. 9. *Protoperidinium variegatum*, Ross Sea: a – ventral view; b – apical view.

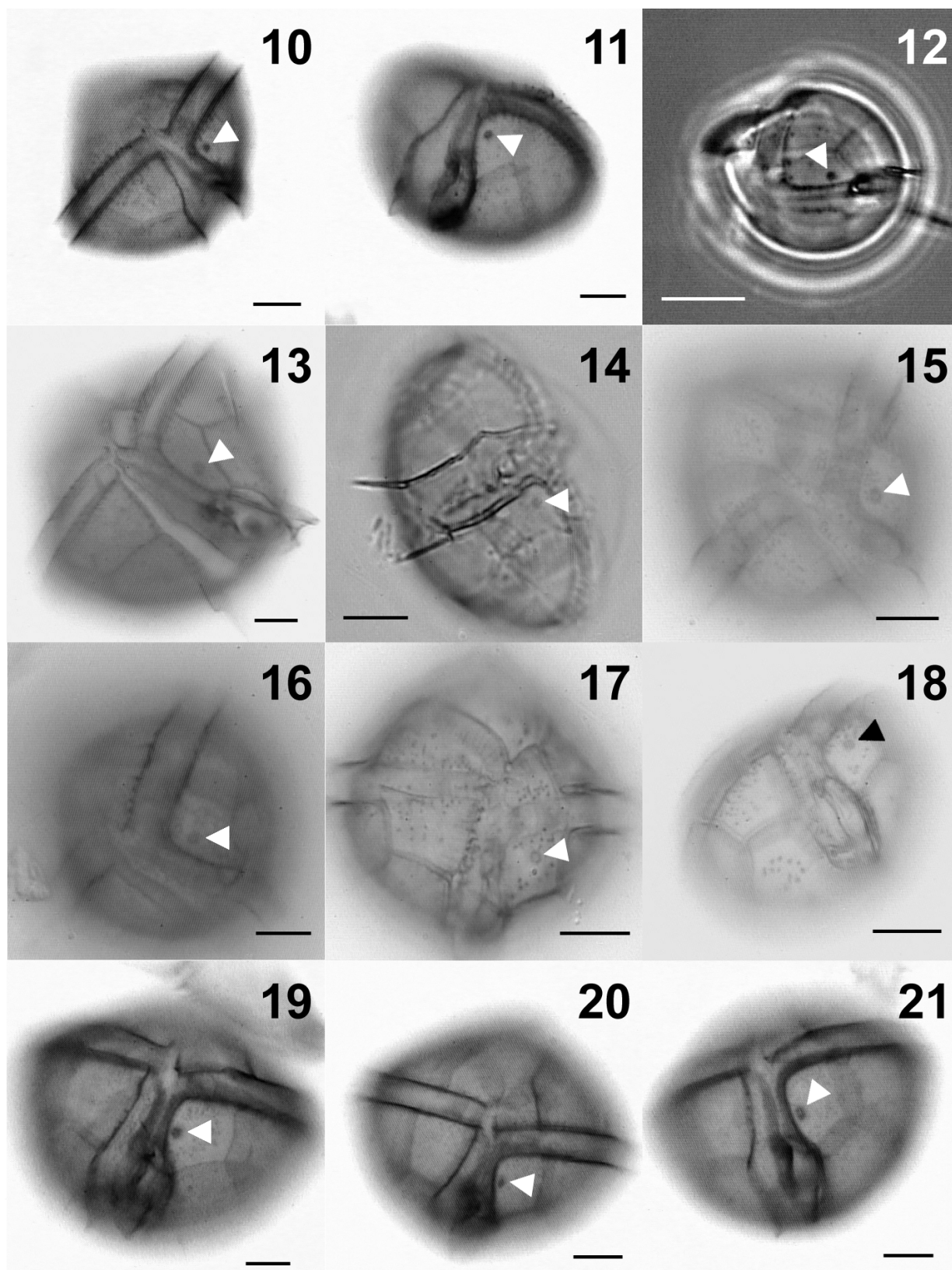


Fig. 10, 11. *Protoperidinium affine*, Ross Sea. Fig. 12. *Protoperidinium ovum*, theca, Gulf of Mexico (phase contrast). Fig. 13. *Protoperidinium pallidum*, SE Mexican Pacific. Fig. 14. *Protoperidinium pellucidum*, hypotheca, NW Mexican Pacific. Fig. 15, 16. *Protoperidinium* sp. 1 (meta-para), Gulf of Mexico. Fig. 17, 18. *Protoperidinium* sp. 2 (hexa-para), Gulf of Mexico. Fig. 19-21. *Protoperidinium variegatum*, Ross Sea.

cidum Balech (Balech, 1971a: 155, pl. 33, fig. 240-242) and *P. aequatoriale* (Balech) Balech (Balech, 1971b: 26, pl. 6, fig. 112-114). However, in none of these species the hypothecal pore was described or illustrated, which makes correct identification of our specimens difficult.

The pore is thought to be present in closely related species and to be a reliable diagnostic feature to differentiate *Protoperidinium* species. Similarities in morphology of the sulcal plates, especially of the anterior (S_a), left (S_l) and right sulcal plates (S_d) between species of group 1 (Balech, 1988) and to a lesser extent of group 2 (Balech, 1975) and group 5 (Balech, 1988) substantiate our suggestion. It is important to note that in all studied cells of the same species the hypothecal pore had the same location on the 1''' plate. Groups 1 and 2, which include the species inhabiting the regions north of the Antarctic Convergence or the Antarctic Ocean, to which they are endemic (*Protoperidinium affine* and *P. variegatum*), seem to represent the geographical vicariants (Okolodkov, 2000). Among all species given in Tables 1 and 2, only *Protoperidinium pellucidum* subsp. *stellatum* sometimes demonstrates 2 or more hypothecal pores described as star-like structures (Balech, 1978, 1988).

In our material, under the objective 40/0.65, the hypothecal pore was clearly seen in all species but *Protoperidinium ovum*, in which the pore was hardly discernible. However, it was easily distinguishable in the empty thecae of *P. ovum*, especially when the negative phase contrast was used. The pore size including a rim around the pore varied between species (1.0 to 3.5 μm) and within the same species. For example, the pore size in *Protoperidinium variegatum* ranged from 1.8 to 3.0 μm . The largest hypothecal pores were observed in *P. pallidum* and *P. variegatum*.

It is interesting to note that groups of dots on the first antapical plate (3 or 4 dots in *Protoperidinium cruciferum* and *Peridinium acutum*), which can be interpreted as the hypothecal pore, were observed by Balech (1971a) in *Protoperidinium mite* (Pavillard) Balech. For this species, two groups of 4 or 5 dots, similar to those in *P. cruciferum*, have been known (the pores are pictured but no comments are given).

In addition, there is another *Protoperidinium* species, *P. cf. retiferum* (Matzenauer) Balech, which has one or two rather large pores on the hypotheca (Balech, 1978, 1988). However, these are located at the base of the antapical horns, on the ventral side of the postcingular plates 1''' and 2''': on the left horn if only one pore is present and on each horn if two pores.

Abé (1981) suggested a secretory function of the hypothecal pore such as that of connecting the pusule system

to the exterior. However, Dodge (1987), who analyzed the possible connection, concluded that at present it was not possible to suggest any function for the hypothecal pore.

Apart from the hypothecal pore located on the 1''' plate, another structure consisting of a group of pores, designated as "a distinctive zone of honey-combed pores" and located on the antapical plate (1''') of the hypotheca of the Peridinales has been observed. Carbonell-Moore (1994) described it in the three new genera of the family Podolampaceae, *Mysticella* Carbonell-Moore, *Garderia* Carbonell-Moore and *Heterobractum* Carbonell-Moore (in the genus *Heterobractum*, a group of pores is pictured but no comments are given).

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