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Are *Protoperidinium knipowitschii* from the Sea of Azov and the Western Mediterranean *P. paulseni* (Dinoflagellata: Peridiniales) Synonymous?

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Abstract

Thecal morphology and morphometry of the planktonic dinoflagellate *Protoperidinium paulseni* (Pavill.) Balech were studied in samples taken in the northwestern Black Sea (Odessa Bay). Using epifluorescence microscopy and SEM, data on the apical pore complex, apical intercalary, sulcal and cingular plates were obtained for the first time; the presence of the hypothecal pore in the 1''' plate is also reported for the first time. The epitheca morphology was clarified (para 1' and hexa 2a plates). Cells are 50.3-65.4 µm long and 38.5-52.4 µm wide (n=15). Light and scanning electron micrographs of the examined cells are presented. A comparison between the original descriptions and illustrations of *P. paulseni*, *P. knipowitschii*, our cells from Odessa Bay, as well as *P. fatulipes* and *P. saltans* (the species mentioned in the literature as morphologically similar to the former two), was made. The results showed that *Protoperidinium knipowitschii* (Usachev) Balech 1974 (basionym: *Peridinium Knipowitschii* Usachev 1927) described from the Sea of Azov can be considered synonymous to *Protoperidinium Paulseni* (Pavill.) Balech 1974 (basionym: *Peridinium paulseni* Pavill. 1909). Data on the geographical distribution of *P. paulseni* are provided.

Introduction

The genus *Protoperidinium* Bergh 1881 is one of the most diverse in terms of the number of species among marine planktonic dinoflagellates (Sournia, 1986; Okolodkov, 2011; Gómez, 2012) and among marine phytoplankton in general. There are 379 currently taxonomically accepted species names of *Protoperidinium* in AlgaeBase (Guiry & Guiry, 2023), as well as eight species of unknown taxonomic position and three unverified names.

Pavillard (1909) described the marine heterotrophic dinoflagellate *Peridinium paulseni* from the Gulf of Lion, the western Mediterranean (Figure 1). The main morphological characters of the species were as follows: (1) ovoid cell outline at the level of the cingulum; (2) cell measurements: 45-50 µm long and 33-35 µm wide (without considering the cingular lists); (3) both epitheca and hypotheca are abruptly narrowing towards their ends; and (4) two divergent spines are very long, and a tiny supplementary spine is curved (note: it is obvious that it is the left sulcal list).

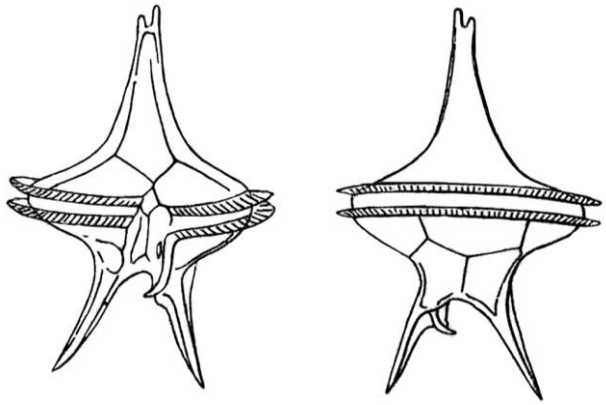

Figure 1. Original line drawings of the new species *Peridinium paulseni* described by Pavillard (1909) from the Gulf of Lion. Left image – ventral view; right image – dorsal view.

Subsequently, Schiller (1937: 271, figure 276) included it in his review. The species had not been mentioned in the literature until Balech (1974) suggested transferring all known marine species of the genus *Peridinium* Ehrenb. to the genus *Protoperidinium* Bergh, including *Peridinium paulseni* – *Protoperidinium paulseni* (Pavill.) Balech (Balech, 1974: 68). Balech ascribed *Protoperidinium paulseni* to the species group with the ortho 1' plate, although in the original description of *Peridinium paulseni* the information about the 1' plate was lacking; he also noted that tabulation of the dorsal side of the epitheca was unknown. Since then, the species has been occasionally reported in the atlas (Delgado & Fortuño, 1991) and the regional species lists (Vilicic *et al.*, 2002; Balkis, 2004; Gómez, 2012; Feyzioğlu & Şahin, 2017; Krakhmalnyi *et al*., 2018), which can be explained by a deficiency in Pavillard's description. Gómez (2005) mentioned *Protoperidinium paulseni* (Pavill.) Balech, noting that *Protoperidinium paulseni* Mangin 1911 and *Protoperidinium paulseni* T.H. Abé 1981 were not synonymous with the former. It is obvious that *P. paulseni* Mangin belongs to the "*Diplopsalis* group" (see Mangin, 1911: 647, figure 2, I-V), and *P. paulseni* T.H. Abé (Abé, 1981: 359, figures 51, 349-354) is similar to the species of the ortho-hexa type, with cingulum ends not displaced and without the antapical horns or spines of *Protoperidinium punctulatum* (Paulsen) Balech or *P. subinerme* (Paulsen) A.R. Loeblich III (see Abé, 1981: 352, figures 49, 326-330; 365, figures 54, 368-374). No distributional records for *Protoperidinium paulseni* (Pavill.) Balech have been available in AlgaeBase (Guiry & Guiry, 2023) to date.

Usachev (1927: 413-415, figures 2, A, B, C and D) described a new species, *Peridinium knipowitschii*, from the samples taken in 1924–1926 in the Sea of Azov (Figure 2). The species was named after the Russian ichthyologist, marine zoologist and oceanographer Nikolai M. Knipovich. According to the description, the cells are elongated, 1.4–1.6 longer than wide, with the epitheca equal or slightly smaller than the hypotheca. The epitheca is conical, with a slender apical horn and strongly concave sides. The apex is slightly shifted to the dorsal side, and the apical pore is wide. The antapical horns are divergent and usually inclined towards the ventral side of the cell, terminated with elongated spines; the horns reach half of the cell width. The margins encircling the sulcus are converted into two wing-shaped appendages. The cingulum is wide, slightly concave, bearing feather-like ribs along both sides. Chromatophores (= chloroplasts) are yellow. Red droplets are present in the cytoplasm. Cell measurements: 50-80 µm long and 45-72 µm wide. The thecal formula includes the R (rhomboid) plate (= the 1' plate), the D (dorsal) plate and four F (apical) plates

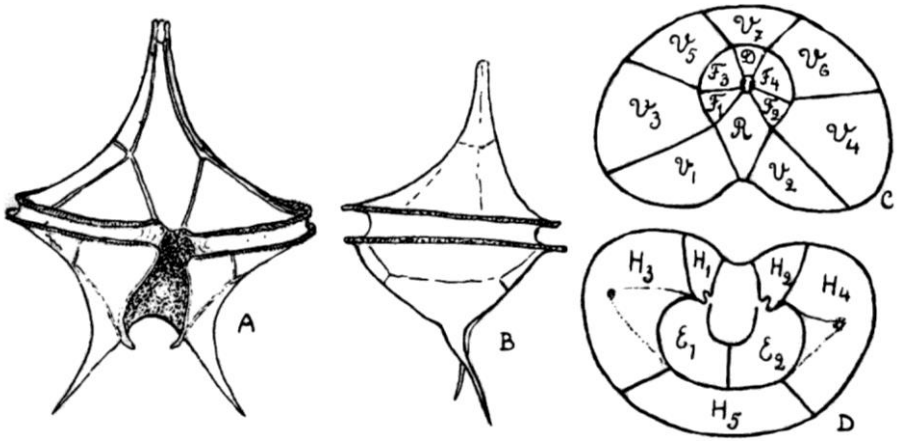

Figure 2. Original line drawings of the new species *Peridinium knipowitschii* described by Usachev (1927) from the Sea of Azov. A – ventral view; B – lateral view; C – apical view; D – antapical view.

(apart from the rhomboid plate), seven or six pre-equatorial (= precingular) plates, five post-equatorial (= postcingular) and two antapical plates. Surprisingly, no intercalary plates were distinguished.

Later, Kiselev (1950: 203) considered these strange features of the *P. knipowitschii* theca; however, he noted that five (not six; presumably by mistake) plates are grouped around the apical pore. In addition, he mentioned that Usachev's species is similar to *Protoperidinium fatulipes* (Kof.) Balech 1974 (= *Peridinium fatulipes* Kof. 1907: 174, plate 5, figure 30). We consider the similarity between *P. paulseni* and *P. fatulipes* superficial and that these species have more differences than features in common. *Protoperidinium fatulipes* is much larger (147 µm long, 100 µm wide), with the epitheca equal to the hypotheca, widely separated (forming a broad arc) and divergent, straight antapical horns not terminated with spines, reticulate thecal plates, the meta 1' plate, and the sulcal lists not projecting posteriorly. Common features between *P. knipowitschii* and *P. fatulipes* are the cell shape with concave sides in ventral view, a slightly ascending cingulum, a long attenuate apical horn, and a slightly cavozone cingulum.

Protoperidinium knipowitschii has been occasionally found in the Sea of Azov and the Black Sea (Pitsyk, 1950, 1963; Kiselev, 1950; Morozova-Vodyanitskaya, 1954; Ivanov, 1959, 1960, 1964, 1965, 1967; Krakhmalnyi, 1995, 2006, 2011; Goméz & Boicenco, 2004; Krakhmalnyi *et al.,* 2006, 2018; Terenko, 2007; Bryantseva *et al*., 2016). However, its records have not been accompanied by drawings or photomicrographs.

Peridinium knipowitschii was transferred to the genus *Protoperidinium* by Balech (1974). He noted that he had already finished the manuscript when he received Usachev's description of *P. knipowitschii* from the Russian phytoplanktologist Victoria V. Zernova. According to Balech, tabulation of the epitheca appears to be incorrect; he commented that the cell shape and Usachev's observation of the cell in apical view made the tabulation of the apical region confusing or indiscernible, which can explain the obvious "lack" of the intercalary plates and the 3' plate. In conclusion, Balech suggests that of six apicals observed by Usachev, three of them are intercalaries. If so, in Usachev's drawing of the theca in apical view, these intercalaries are F4, D and F3, which, in fact, are equivalent to the 1a, 2a and 3a plates, respectively. Based on his arguments and suggestions and taking into account the cell shape of *P. knipowitschii* that is similar to that of *P. saltans* (Meunier) Balech, Balech concludes that Usachev's species can be close to the latter, and it is likely ortho-quadra (i.e., the 1' plate is ortho and the 2a plate is quadra, bordering with the four contiguous plates). However, it is known that Meunier tended to illustrate *Peridinium* species later transferred to *Protoperidinium* by Balech (1974) with the ortho 1' plate.

Unlike *P. paulseni*, *P. knipowitschii* and our cells, those of *P. saltans* are significantly larger, the epitheca and hypotheca equal in size, with a rounded central part (convex sides in ventral and side views) and a short apical horn, a planozone descending cingulum, the 2a of quadra type, three intercalaries almost equal in size, with very curved antapical horns notably deflected posteriorly-laterally, and without emerging sulcal lists (Meunier 1910: 26, pl. 1bis, figures 9-14). Moreover, it is worth mentioning that neither *P. fatulipes*, nor *P. saltans* have been reported from the Black Sea (Krakhmalnyi *et al.,* 2018). In addition, Balech (1974: 57) notes that *P. saltans* has a very variable tabulation, sometimes with only two intercalaries or six precingulars. Gómez (2005: 199) included *Protoperidinium knipowitschii* in his list, mentioning that the species is a taxon "of very doubtful validity".

As it is shown in this study, *Protoperidinium paulseni* and *P. knipowitschii* are morphologically very similar, and it is almost impossible to distinguish between them. It has been suggested that these two names belong to the same species. To test this hypothesis, a study based on samples taken from the northwestern Black Sea was performed.

Materials and Methods

Samples were collected in the northwestern Black Sea (Odessa Bay) where physical-chemical conditions are similar to those in the type locality of *P. knipowitschii* (Sea of Azov). The following sampling sites were monitored weekly during 2016–2020: Malyi Fontan (46°26'28.31" N, 30°46'22.04" E; from the pier and a small boat) and Arcadia (46°25'31.48"N, 30°46'06.82"E; from the pier and a small boat). The average salinity at the sampling sites was 12–17 ‰, which is close to the salinity values in the southern regions of the Sea of Azov (Mokievskij *et al*., 2019). Samples were taken with a 6-liter plastic bottle from the surface layer and fixed with formaldehyde to a final concentration of 4%. A hand net of 60 µm mesh size was also used. In the laboratory, the samples were concentrated using a reverse-filtration technique (Fedorov, 1979).

Morphological observation of the dinoflagellate cells was performed with an Olympus BX51 compound microscope in a bright field, using Nomarski contrast and epifluorescence in combination with Calcofluor White M2R to visualize thecal plates (Fritz & Triemer, 1985). The UPlanFLN 40x/0.67 and UPlanFLN 100x/1.30 Oil objectives were used. Micrographs were taken with a Canon EOS 1000D digital reflex 10.1-megapixel camera. Images were processed using an MS Adobe Photoshop CS5 program. Cells were measured using the AmScope 3.7 program, and statistics were carried out using the Statistica 4.5 package.

Additionally, some samples were examined under a field emission scanning electron microscope (FE-SEM) Sigma 300 (Carl Zeiss Microscopy GmbH, Jena,

Germany). Sample preparation for SEM followed the protocol of Chomérat & Coutè (2008).

Results and Discussion

A redescription of *Protoperidinium paulseni* originally described from the Gulf of Lion, the western Mediterranean Sea, is given below, based on the samples collected from the northwestern Black Sea.

Division Dinoflagellata (Bütschli 1885) Fensome et al. 1993

Class Dinophyceae Pascher 1914

Order Peridiniales Haeckel 1894

Family Protoperidiniaceae Balech 1988 nom. cons.

Genus *Protoperidinium* Bergh 1881

Protoperidinium paulseni (Pavill.) Balech 1974 (Figures 3-6)

Basionym: *Peridinium paulseni* Pavill. 1909: 280, Figure 2, A and C.

Synonyms: *Peridinium Knipowitschi* Usachev 1927: 413-415, Figure 2, A, B, C and D; *Protoperidinium knipowitschii* (Usachev) Balech 1974: 68, 73.

Description. Cells subpentagonal, the epitheca is slightly larger than the hypotheca, conical, with concave

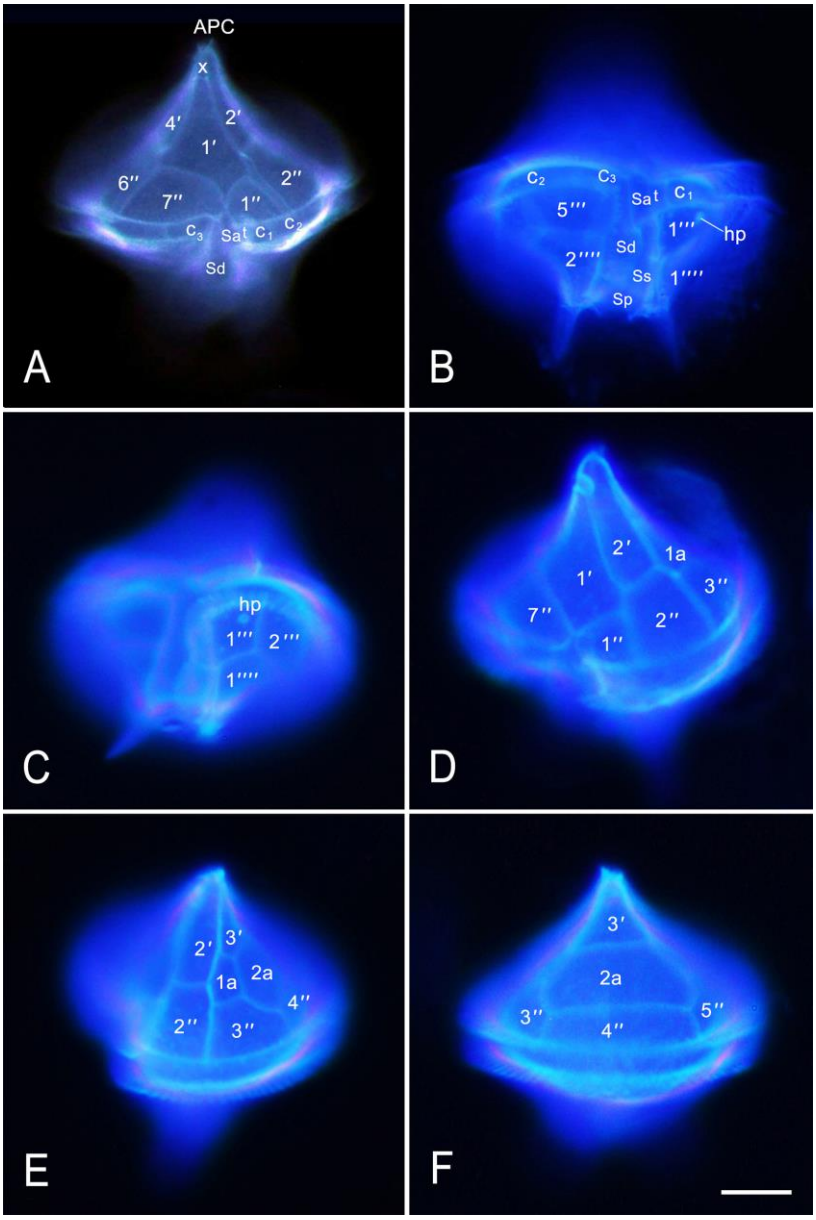

Figure 3. Theca of *Protoperidinium paulseni* in epifluorescence microscope. A – ventral-apical view, showing the para 1' plate, the slightly ascending cingulum, the apical pore complex (APC) consisting of the pore plate and the canal plate (x); B – ventral-antapical view, showing the sulcal plates (Sa – anterior sulcal plate, Sd – right sulcal plate; Sp – posterior sulcal plate; Ss – left sulcal plate) and the hypothecal pore (hp); C – ventral-antapical-left side view, showing the hypothecal pore, a wide left sulcal list along the 1‴ and 1⁗ plates and ventrally deflected antapical spines; D – apical-ventral-left side view, showing a part of the epithecal plates; E – apical-left side view, showing a smaller 1a plate; F – dorsal-apical view (focused on the 2a plate), showing the hexa 2a plate. Abbreviations: 1'-4' – apical plates; 1a and 2a – intercalary plates; 1"-7" – precingular plates; c_1-c_3 – cingular plates; t – transitional plate. Scale bar (A-F): 10 µm.

sides in ventral view and a relatively long apical horn (Figures 3D, 6A and 6B), with reticulated theca (Figure 6A-D). The apical pore complex consists of the Po plate and a subrectangular canal plate (Figures 3A and 6A). The 1' plate is of para-type (Figures 3A, 4E, 5A, 6A and 6C), slightly asymmetrical in relation to the longitudinal axis, with the angles slightly below the median line in ventral view of the cell. The 1a and 3a plates are smallest on the epitheca, pentagonal (Figures 3E, 4A, 4B and 5C-E). The 2a is of hexa-type, subtrapezoidal, large, about twice as wide as the 4" plate (Figures 3F, 4A, 5B, 5D, 5E, 6B and 6C). The 1" and 3" are the smallest among the precingulars (Figures 3A, 3D and 5A). The 7" plate forms a characteristic triangular indentation adjacent to the Sa, Sd and c_3 plates (Figures 3A, 5A, 6A and 6D). The cingulum is cavozone, wide, ascending, with its ends displaced about 0.5 girdle width (Figures 3A, 3B, 5A, 6A and 6D), bordered by two cingular lists with numerous ribs (Figures 4E, 4F, 6A and 6C). The sulcus slightly enters the epitheca with the Sa plate, forming a shallow notch

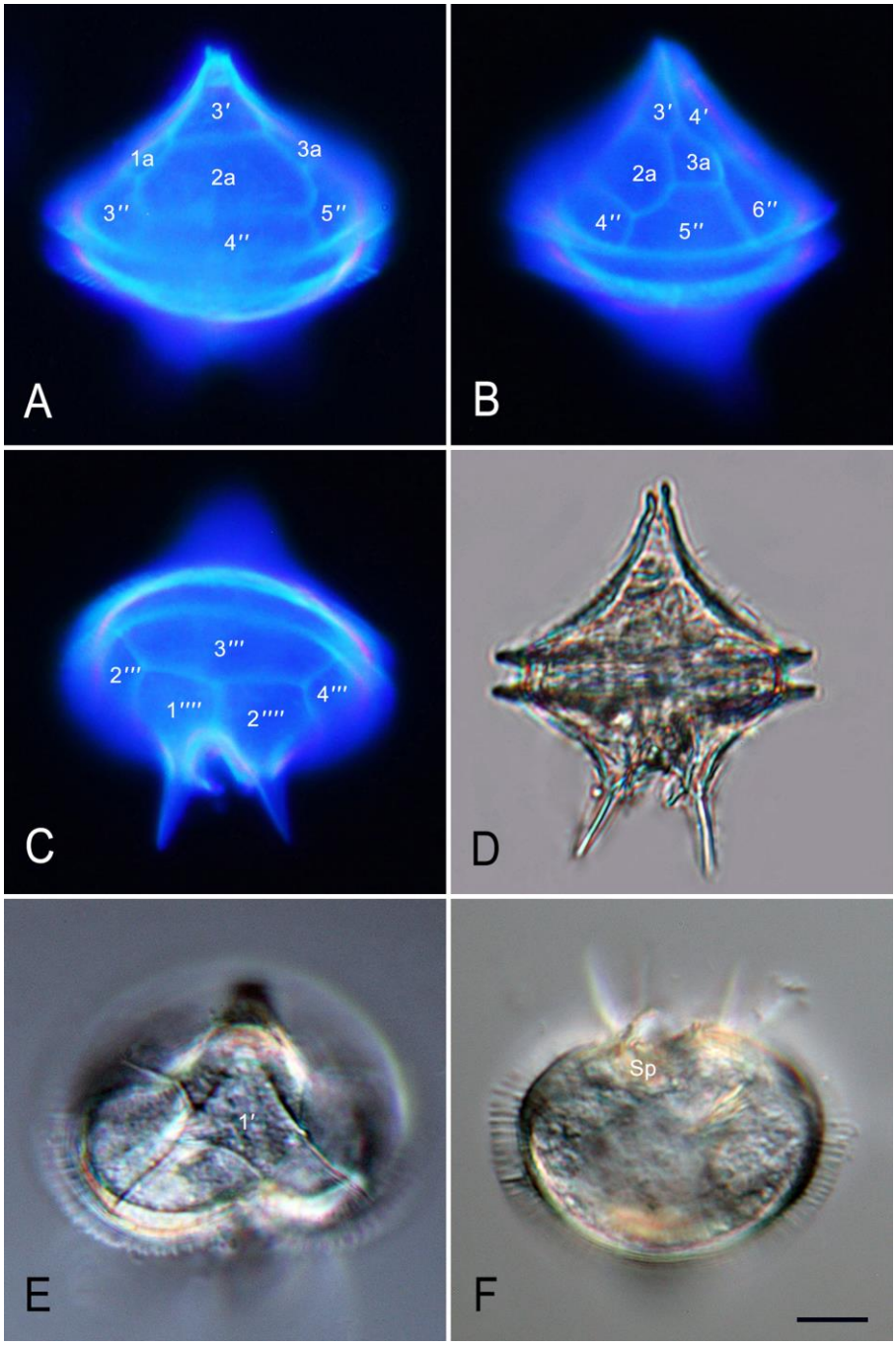

Figure 4. Theca of *Protoperidinium paulseni* in epifluorescence microscope (A-C) and in bright field (D-F). A – dorsal-apical view, showing three intercalary plates; B – dorsal-apical-right side view. C – dorsal-antapical view; D – ventral view, showing the outline of the cell with its diagnostic characteristics; E – apical-ventral view, showing the para 1' plate; F – antapical view (a mirror image), showing a ventrally compressed cell with a rather wide cingular list with numerous ribs and ventrally deflected antapical spines. Abbreviations: 1', 3' and 4' – apical plates; 1a-3a – intercalary plates; 3"-6" – precingular plates; 2"'-4"' – postcingular plates; 1"" and 2"" – antapical plates; Sp – posterior sulcal plate. Scale bar (A-F): 10 µm.

(Figures 3A, 3D, 5A, 6A and 6D), with the left sulcal list emerging in a way that it can be confused with a spine (Figures 4D, 5A and 5B). The hypotheca tapers rather abruptly toward the antapex (Figures 4D, 5A and 5B). The antapical horns are situated close to each other, relatively long, slightly divergent, terminating with slender spines and somewhat deflected to the ventral side of the cell (Figures 3B, 3C, 4C, 4D, 4F and 5A-C). The arrangement of thecal plates, in general, is symmetrical in relation to the longitudinal axis of the cell (Figures 3A, 3F, 4A, 4C and 6A-C). The trichocyst pores are irregularly dispersed throughout the plates, denser along the distal margin of the precingular plates (Figures 6C and 6D). The 1”’ usually bears a larger hypothecal pore closer to the cingulum and the 2”’plate (Figures 3B, 3C and 6A); occasionally, there are two larger pores on the 1”’ closer to the cingulum, and in some cases another two larger pores were observed on the 5”’plate, positioned similarly (Figure 5A). Cytoplasm is colorless or light yellow, with numerous tiny “bubbles”. Thecal formula: Po, x, 4', 3a, 7'', 3C+t, 6S, 5''', 2'''' (although not all sulcal plates were observed). Size: 50.3–65.4 µm long and 38.5–52.4 µm wide (n=15).

Distribution: western Mediterranean (Pavillard, 1909; Delgado & Fortuño, 1991), Adriatic Sea (Vilicic & Marasovic, 2002), Sea of Marmara (Balkis, 2004), Sea of Azov (Usachev, 1927; Kiselev, 1950; Krakhmalnyi, 2011), Black Sea (Goméz & Boicenco, 2004; Krakhmalnyi *et al*., 2018). It should be noted that only a third of the reports of the species in the literature are based on original findings, and the rest are compiled from the published sources.

Affinities. Our specimens are more similar in cell shape to *P. paulseni* (Figure 1). They also share some common features with *P. knipowitschii* (Figure 2). However, a comparison of tabulation between these three entities is not feasible: both Usachev’s (1927) and Pavillard’s descriptions (1909) are deficient in that they lack information on the 1’ plate and 2a plate (if any) types, some of the most important morphological

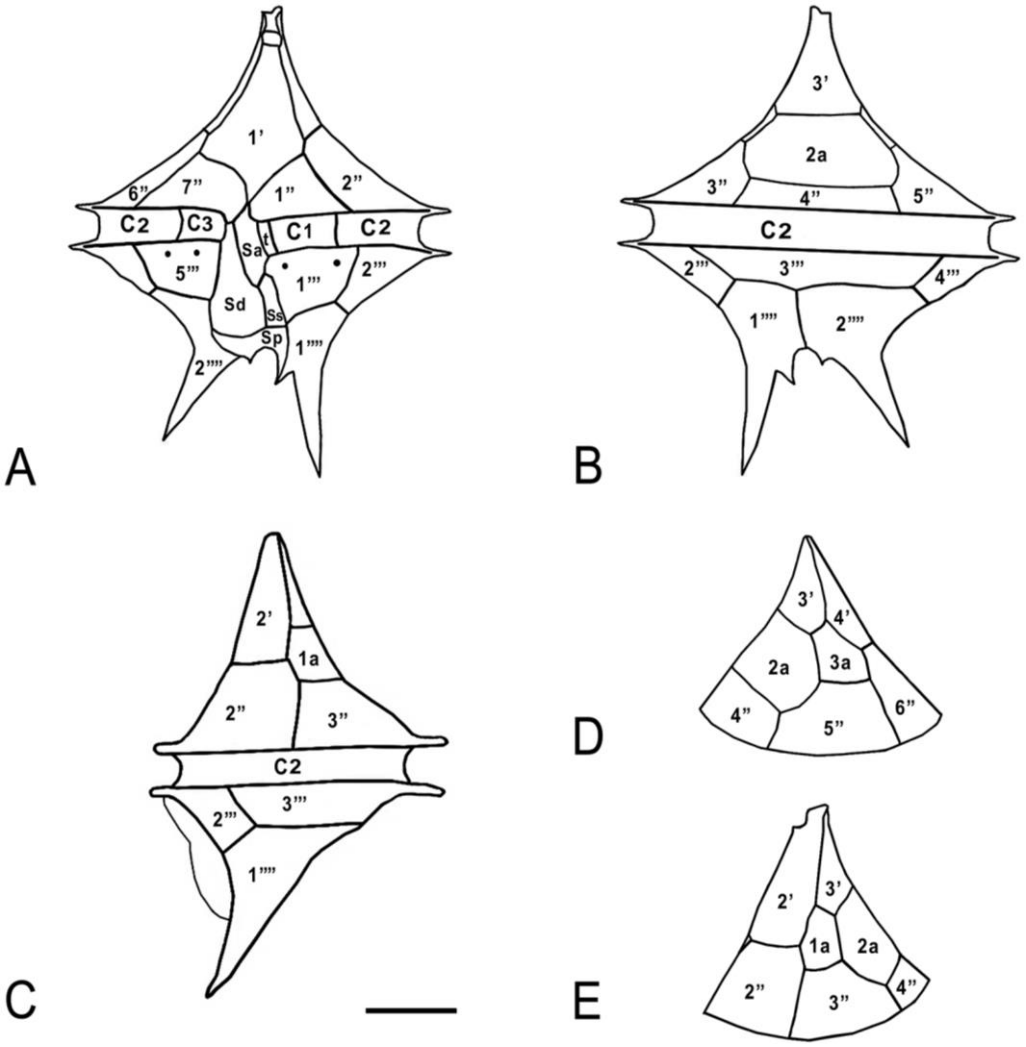

Figure 5. Line drawings of *Protoperidinium paulseni* from Odessa Bay. A – ventral view, four hypothecal pores are seen near the cingulum, on plates 1”’ and 5”’; B – dorsal view; C – left side view; D – right side view of the epitheca; E – left side view of the epitheca. Abbreviations: 1’-4’ – apical plates; 1a-3a – intercalary plates; 1”-7” – precingular plates; c_1-c_3 – cingular plates; t – transitional plate; Sa – anterior sulcal plate, Sd – right sulcal plate, Sp – posterior sulcal plate, Ss – left sulcal plate. Scale bar (A-E): 10 µm.

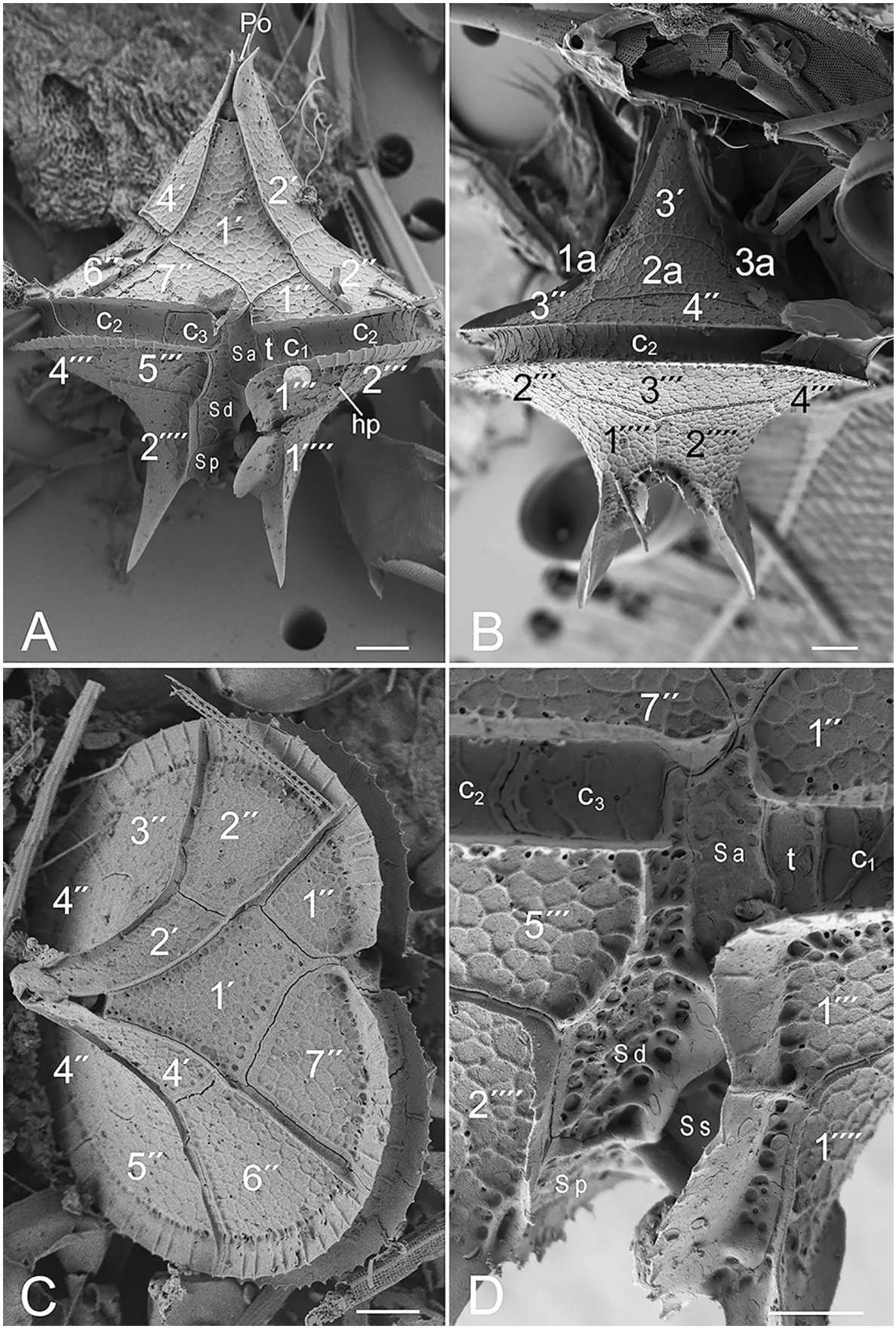

Figure 6. Theca of *Protoperidinium paulseni* in scanning electron microscope. A – ventral view; B – dorsal view; C – apical-ventral view, showing the epithecal plates; D – the sulcal area and adjacent plates in ventral view. Abbreviations: 1′-4′ – apical plates; 1a-3a – intercalary plates; 1″-7″ – precingular plates; c_1-c_3 – cingular plates; hp – the hypothecal pore; Po – the pore plate; t – transitional plate; Sa – anterior sulcal plate, Sd – right sulcal plate, Sp – posterior sulcal plate, Ss – left sulcal plate. Scale bar (A-D): 5 μm.

characteristics of the theca that are used to identify the taxa from the genus *Protoperidinium* to the species level. Moreover, our cells from Odessa Bay are almost symmetrically rhomboid, and the cell pictured by Pavillard has the connections along the sutures between the 1' plate and the 1" and 7" plates noticeably shorter (Figure 1, left). The cell outline of our cells in ventral/dorsal view is very similar to Pavillard's drawings; in particular, the shorter hypotheca is one of the most characteristic features (Figure 1).

The position of the hypothecal pore on the 1"' plate near the suture separating it from the 2"' plate in our species is unique. It is different from all *Protoperidinium* species studied by us previously (Okolodkov, 2003): *P. affine* (Balech) Balech and *P. variegatum* (Peters) Balech from the Ross Sea, *P. dodgei* Okolodkov from the NE Atlantic, *P. ovum* (J. Schiller) Balech, *Protoperidinium* sp. 1 and *Protoperidinium* sp. 2 from the Gulf of Mexico, *P. pellucidum* Bergh from the NW Mexican Pacific, and *P. pallidum* (Ostenf.) Balech and *P.* cf. *cruciferum* Balech from the SE Mexican Pacific. In addition, Balech (1988: 119, plate 49, figures 8-14) described *P. pellucidum* ssp. *stellatum* Balech from the SW Atlantic with a characteristic hypothecal pore (sometimes with a few) closer to the sulcal area and surrounded by ribs. However, unlike the examined species from the Black Sea, this taxon has a planozone cingulum and different cell outline (concave sides of the hypotheca in ventral/dorsal view and without a notch at the antapex), although they share some features, such as the plate pattern (para-hexa), a slightly ascending cingulum, an oblique curved pseudospine on the left side of the hypotheca (the membrane of the Ss platelet), two long divergent spines and a moderately developed apical horn. Therefore, we consider *P. paulseni* and *P. pellucidum* ssp. *stellatum* related species.

In the samples from Odessa Bay, we found the cells that could be ascribed to both *Protoperidinium paulseni* and to *P. knipowitschii* simultaneously. In only one sample some cells were similar to those pictured by Pavillard (1909) and others to those illustrated by Usachev (1927) (Figures 1 and 2). Morphological differences were not in distinguishing characteristics, but in morphometrical features: cells 45–50 µm long and 33–35 µm wide in Pavillard, 55–80 µm long and 45–72 µm wide in Usachev, 50.3–65.4 µm long, and 38.5–52.4 µm wide from Odessa Bay, and there were slight differences in cell shape. According to the original descriptions, *Protoperidinium paulseni* has smaller and more slender cells (Figure 1), while *P. knipowitschii* appear to be more robust, with a somewhat larger central part of the cell (Figure 2). These subtle differences can be explained by the cell age, developmental stage or environmental conditions (water temperature, salinity, nutrients, etc.), and they are within the infraspecific variation. Other factors, such as position of the studied cell in relation to the observer and drawing capacity, cannot be excluded. Unfortunately, there are no published photographs of the cells ascribed to these two species.

Usachev's line drawings in ventral and apical views (Figure 2: Usachev's figures A and C) do not allow us to determine the type of the 1' plate (this plate is shown with the connections with the adjacent plates of "neutra" type distinguished in the description of the 2a plate; see Okolodkov, 2008), which is an important taxonomic feature for dividing the genus *Protoperidinium* into sections or unclassified units. Moreover, the position of the apex described by Usachev as slightly shifted to the dorsal side does not correspond to his drawing in the right-sided view (Figure 2: Usachev's figure B): the apex is clearly shifted to the ventral side.

Conclusion

The inability to obtain and cultivate the cells of both *Protoperidinium knipowitschii* and *P. paulseni* from the type localities would preclude application of molecular techniques at this time. A comparative morphological analysis instead is a priority. We conclude that, although Usachev's description of *P. knipowitschii* is deficient, *Protoperidinium paulseni* and *P. knipowitschii* cannot be distinguished morphologically and are thus synonyms, and *Protoperidinium Knipowitschii* (Usachev) Balech 1974 and its basionym (*Peridinium Knipowitschi* Usachev 1927) are junior synonyms of *Protoperidinium paulseni* (Pavill.) Balech 1974 (basionym: *Peridinium Paulseni* Pavill. 1909).

Ethical Statement

Not applicable

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Author Contribution

AFK: concept of the manuscript, literature analysis, sampling, microscopy, data analysis, manuscript writing; YBO: concept of the manuscript, literature analysis, data analysis, manuscript writing, preparation of illustrations; GVT: literature analysis, sampling, microscopy, data analysis, review and editing; MAK: literature analysis, microscopy, data analysis, preparation of illustrations, manuscript writing and editing. All the authors have seen the final version of the manuscript and provided their approval for the submission.

Conflict of Interest

The authors declare that they have no known competing financial or non-financial, professional, or

personal conflicts that could have appeared to influence the work reported in this article.

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