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Islandinium pacificum sp. nov., a new dinoflagellate cyst from the upper Quaternary of the northeast Pacific

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ABSTRACT

Round brown process-bearing cysts (RBPC) produced by dinoflagellates (Dinophyceae) occur as an important part of assemblage diversities in seafloor sediments worldwide. Here a new species, *Islandinium pacificum*, is described from surface sediment samples from coastal waters of British Columbia (Canada). Additional observations are made on material from the Holocene of Kyuquot Sound (Vancouver Island, Canada) and the Eemian of the Vøring Plateau (North Atlantic). The cysts have a smooth wall and bear acuminate processes with barbs. Incubation experiments reveal an affinity with the motile stage *Protoperidinium mutsuense*. The ecology of the new species is specified.

KEYWORDS

Round brown process-bearing cyst; taxonomy; cyst–theca relationship; Pacific Ocean; Atlantic Ocean; Saanich Inlet

1. Introduction

More than 2000 species of dinoflagellates are recognized (Gómez 2012), and more than 200 of them are known to form a resting cyst as part of their life cycle (Head 1996). Some of these dinoflagellate cysts are highly resistant to physical and chemical degradation, which provides an excellent fossilization potential. Fossil dinoflagellate cysts have been applied in a wide range of geological studies, mainly involving biostratigraphy and paleoenvironmental reconstructions (e.g. Dale 1996; de Vernal et al. 2001; Marret et al. 2001; Louwye and Laga 2008; Van Nieuwenhove et al. 2008; Holzwarth et al. 2010; Riding et al. 2010; Limoges et al. 2018; Pospelova et al. 2015). The cyst stages differ morphologically from the motile stages and a dual taxonomy exists in which cyst stages and motile stages are given names in parallel. This practice grew historically from the fact that the dinoflagellate origin of cysts recovered from sedimentary records did not become obvious until the 1960s (e.g. Evitt and Davidson 1964; Wall 1965) and that the motile affinity of a cyst is usually unknown at the moment of discovery of the latter. Both incubation experiments and molecular analysis can establish the relation between motile and cyst stages for a dinoflagellate species. Dual taxonomy is still often poorly resolved, however, and in order to fully understand the information confined in dinoflagellate cyst records, taxonomic issues need to be resolved first.

Round brown process-bearing cysts (RBPCs) is a collective term for dinoflagellate cysts with a (sub)spherical central body bearing processes, and is a more correct name for what has been previously called round brown spiny cysts (RBSCs;

e.g. Potvin et al. 2017), as spines are defined as acuminate processes (i.e. tapering to a pointed distal end) (e.g. Fensome et al. 1993). RBPCs constitute an important morphological group in many dinoflagellate cyst assemblages in surface sediments from the northern Pacific and Atlantic oceans (e.g. Rochon et al. 1999; Pospelova et al. 2008; Richerol et al. 2012; Radi et al. 2013; Zonneveld et al. 2013; Heikkilä et al. 2014; Gurdebeke et al. 2018; Limoges et al. 2018), and in Holocene records (e.g. Bonnet et al. 2010; Ouellet-Bernier et al. 2014; Richerol et al. 2014; Gibb et al. 2015; Bringué et al. 2016; Li et al. 2017). RBPCs generally constitute minor parts of cyst assemblages in temperate zones (e.g. Pospelova et al. 2008; Gurdebeke et al. 2018), but they may dominate assemblages at higher latitudes (e.g. Head et al. 2001; Richerol et al. 2012; Limoges et al. 2018).

RBPCs are a polyphyletic group and belong to several motile-based genera. They have been primarily related to the order Peridiniales, and at the subfamily level to the Protoperidiniadeae and Diplopsalioideae (Table 1). More specifically, the *Monovela* clade of the Protoperidinioideae contains RBPCs in the subclades *Monovelum*, *Archaeperidinium* and *Americanum* (e.g. Potvin et al. 2017). Within the Diplopsalioideae, a number of RBPC species are associated with several genera (e.g. *Niea*, *Qia*). Finally, RBPCs have also been observed within another order, the Gymnodiniales, notably cysts produced by *Polykrikos hartmannii* (e.g. Matsuoka and Fukuyo 1986) and by *Gyrodinium resplendens*, though the latter do not consistently bear processes (Skovgaard 2000).

Two cyst-based genera of RBPCs were erected, *Echinidinium* (Zonneveld 1997) and *Islandinium* (Head et al.

Table 1. Overview of currently known process-bearing round brown cysts.^a

Motile stage	Cyst stage	Sequence	Phylogeny	Archeopyle	Reference
–	' <i>Echinidinium aculeatum</i> '	No	?	Split	Zonneveld (1997)
–	<i>Echinidinium bispiniformum</i>	No	?	Split	Zonneveld (1997)
–	<i>Echinidinium delicatum</i>	No	?	Split	Zonneveld (1997)
–	<i>Echinidinium granulatum</i>	Yes	Monovela clade, Monovelum subgroup (unpublished)	Split	Zonneveld (1997)
–	<i>Echinidinium karaense</i>	Yes	Monovela clade, Monovelum subgroup	Split	Head et al. (2001), Potvin et al. (2017)
–	' <i>Echinidinium transparantum</i> '	No	?	Split	Zonneveld (1997)
–	<i>Echinidinium zonneveldiae</i>	No	?	Split	Head (2003)
–	–	Yes	Monovela clade, Monovelum subgroup	Split	Mertens et al. (2015)
? <i>Protoperidinium lewisiae</i>	<i>Islandinium brevispinosum</i>	No	?	3 apical plates	Pospelova and Head (2002), Liu et al. (2013)
–	<i>Islandinium minutum</i> subsp. <i>minutum</i>	Yes	Monovela clade, Americanum subgroup	3 apical plates	Head et al. (2001), Potvin et al. (2013), Mertens et al. (2013)
–	<i>Islandinium minutum</i> subsp. <i>barbatum</i>	Yes	Monovela clade, Americanum subgroup	3 apical plates	Potvin et al. (2017)
–	<i>Islandinium?</i> <i>cezare</i>	No	?	Not clear	Head et al. (2001)
<i>Protoperidinium fukuyoi</i>	' <i>Islandinium tricingulatum</i> '	Yes	Monovela clade, Americanum subgroup	3 apical plates	Mertens et al. (2013)
<i>Protoperidinium tricingulatum</i>	–	Yes	Monovela clade, Americanum subgroup	Split between apical and intercalary plates	Kawami et al. (2009)
<i>Protoperidinium haizhouense</i>	? <i>Islandinium brevispinosum</i>	Yes	Monovela clade, Americanum subgroup	Split between apical and intercalary plates	Liu et al. (2013)
<i>Archaeperidinium bailongense</i>	–	Yes	Monovela clade, Archaeperidinium subgroup	Theropyle, intercalary 2a	Liu et al. (2015a)
<i>Archaeperidinium constrictum</i>	–	Yes	Monovela clade, Archaeperidinium subgroup	Theropyle, intercalary 2a	Liu et al. (2015a)
<i>Archaeperidinium minutum</i>	–	Yes	Monovela clade, Archaeperidinium subgroup	Theropyle, intercalary 2a	Yamaguchi et al. (2011), Mertens et al. (2012b, 2013), Matsuoka and Head (2013), Liu et al. (2015)
<i>Archaeperidinium minutum</i> sensu Wall & Dale 1968	–	No	?	Theropyle, intercalary 2a	Wall and Dale (1968)
<i>Archaeperidinium saanichi</i>	–	Yes	Monovela clade, Archaeperidinium subgroup	Theropyle, intercalary 2a	Mertens et al. (2012b)
<i>Archaeperidinium monospinum</i>	–	No	?	Theropyle, intercalary 2a	Zonneveld and Dale (1994), Potvin et al. (2013)
<i>Niea acanthocystab</i>	' <i>Echinidinium</i> type'	Yes	Diplopsalioideae	Split	Kawami et al. (2006), Mertens et al. (2015)
<i>Qia lebouriae</i>	–	Yes	Diplopsalioideae	Theropyle, intercalary 1a	Liu et al. (2015b), Mertens et al. (2015)
<i>Diplopelta symmetrica</i>	–	No	Diplopsalioideae	Split	Dale et al. (1993)
<i>Cochlodinium</i> sp. 2	–	No	?	?	Matsuoka and Head (2013)
<i>Polykrikos hartmannii</i>	–	No	Gymnodinales	Split	Fukuyo (1986)
<i>Gyrodinium resplendens</i>	–	No	Gymnodinales	?	Hoppenrath et al. (2010)

^aStrictly speaking, round brown spiny cysts refer to cysts with acuminate processes.^b*Diplopelta parva* = *Niea acanthocysta*.

2001), differing mainly by their archeopyle type. The genus *Echinidinium* was erected by Zonneveld (1997) for spiny round brown cysts with a chasmic archeopyle (i.e. a split), while Head et al. (2001) defined the genus *Islandinium* for RBPCs with a saphopylic archeopyle reflecting three apical plates (2', 3' and 4'). Potvin et al. (2013) emended the definition of *Islandinium* to include species with a theropylic archeopyle which ruptures along the same three apical plates, such as cysts of *Protoperidinium tricingulatum*, albeit in doing so Potvin et al. (2013) invalidly transferred the cyst of *P. tricingulatum* to *Islandinium*. Subsequent molecular research found a placement for both cyst-based genera in the *Monovela* clade of the genus *Protoperidinium* (Mertens et al. 2013; Potvin et al. 2013, 2017) (Table 1).

Here, a new dinoflagellate cyst species is described which was first recorded in Ocean Drilling Program (ODP) Hole 893 A from the Santa Barbara Basin (southern California) as *Echinidinium* spp. indet and illustrated in auxiliary material by Pospelova et al. (2006, S3, figure 4). Shortly after, it was documented from the Eemian (MIS 5e) of the Norwegian Sea as Protoperidinioid cyst type A by Van Nieuwenhove et al. (2008, supplementary data) and illustrated as Protoperidinioid indet. cyst type A (Van Nieuwenhove 2008, plate 9, figure 7–12 and plate 10, figure 1–12). This species was also illustrated as *Echinidinium?* sp. A, by Radi et al. (2013). The conservation of this cyst type in the Eemian deposits was unfavorable because of dirt clogging of the processes and folding of the cysts. Here, well-preserved and fresh new specimens of this cyst type were observed in modern and Holocene sediments from the northeast Pacific Ocean, allowing further detailed examination, incubation experiments, and the erection of a new species.

2. Materials and methods

The cysts were extracted from surface sediments from Saanich Inlet (SE Vancouver Island; Figure 1A, sites 1–3; see Mertens et al. (2012a) for sampling details for sites 1 and 2), Oak Bay (Figure 1A, site 4) and the Strait of Georgia (British Columbia, Canada; Figure 1A, site 5) (Table S1). Holocene sediments were collected in a core (2012002PCG133; Figure 1A, site 6) from Kyuquot Sound (NW Vancouver Island; Gurdebeke et al. unpub. data).

The sediment samples were treated following a palynological preparation method (e.g. Pospelova et al. 2010). Sediment subsamples were dried for approximately 1 week at $\sim 40^\circ\text{C}$ and weighed. A known number of exotic marker grains (*Lycopodium clavatum* spores) was added (1 tablet of batch #177745) for absolute abundance estimations (e.g. Mertens et al. 2009, 2012a). The samples were treated with 10% hydrochloric acid (HCl) at room temperature for the removal of carbonates (Price et al. 2016). After rinsing with demineralized water, samples were sieved through a $120\ \mu\text{m}$ mesh and captured on a $15\ \mu\text{m}$ mesh to separate from coarse and fine fractions. Next, the samples were treated for a couple of days with $\sim 50\%$ hydrofluoric acid at room temperature for the removal of silicates. Possible newly formed fluorosilicates were removed by using a second round of HCl treatment. After repeated rinsing with demineralized water and sonication, the residue was collected on a screen with a

$15\ \mu\text{m}$ mesh size. One or two drops of the residue were mounted in glycerine jelly and covered with a cover slip.

Morphological (light microscopy, LM; and scanning electron microscope, SEM) observations were made on cysts retrieved from residues prepared palynologically from Eemian sediments in core M23323-1 from the Vøring Plateau (Norwegian Sea, Figure 1B, site 7), as described in Van Nieuwenhove et al. (2011). Photomicrographs of Holocene cysts from Kyuquot Sound were made on a Zeiss Axioskop 2 plus transmitting light microscope (Department of Geology, Ghent University) with $1000\times$ magnification and equipped with an MRC 5 camera. Photomicrographs of modern cysts from Saanich Inlet and the Strait of Georgia were taken on a Nikon Eclipse 80i transmitting light microscope with a Nikon digital sight DS camera head and control unit (Nikon, Tokyo, Japan) at $1000\times$ magnification (University of Victoria, Canada), and on an Olympus BX51 with a digital sight DS-1L 1 module (Nikon, Tokyo, Japan). Photomicrographs of the Eemian specimens were taken on a Zeiss Axiophot microscope and Axiocam camera at $1000\times$ magnification (Geomar Helmholtz Centre for Ocean Research Kiel, Germany). For SEM observation of cysts from modern sediments, residue was used from Saanich Inlet, Stn. 2 (Figure 1A) (UVic 09-659) sampled on 19 May 2009 at a depth of 215 m. The residue was washed with distilled water and dehydrated in a graded ethanol series (30 to 100% in six steps), critical-point-dried with carbon dioxide (CO_2 , CPDBal-Tec 030), glued onto a stub, sputter-coated with platinum/palladium for 90 s using a JFC-2300 HR (JEOL, Tokyo, Japan) and examined using a SEM JEOL 6330F.

For field-emission SEM imaging of cysts from the Eemian of the Vøring Plateau, cysts were picked from the residue and mounted on polycarbonate membrane filters (Millipore, Billerica, MA, USA, GTTP Isopore, $0.22\ \mu\text{m}$ pore size) and sputter-coated with gold. The images were made with a Zeiss SIGMA300 Gemini field emission SEM at the Station de Biologie Marine (Concarneau, France).

To obtain cysts of *Islandinium pacificum* sp. nov. for incubation studies, surface sediment samples containing RBPCs were collected at two locations around southern Vancouver Island, British Columbia, Canada, in October 2011: (i) Oak Bay (Figure 1A, site 4) and (ii) the VENUS site in Patricia Bay, Saanich Inlet (Figure 1A, Stn. 3). All samples were temporarily stored in plastic containers in a refrigerator at 4°C . In situ sea-surface salinities (SSSs) and sea-surface temperatures (SSTs) were measured when collecting samples (Table S1).

A volume of $\sim 0.5\text{--}1.0\ \text{cm}^3$ of wet sediment was immersed in filtered seawater and, after 1 min of ultrasonication using an As OneTM (As One Corp., Osaka, Japan) US2R ultrasonic bath, the sediment was rinsed through a metallic $20\ \mu\text{m}$ mesh calibrated SanpoTM (Sanpo, Tokyo, Japan) sieve using filtered seawater. From this residue, the cyst fraction was separated using the heavy liquid sodium polytungstate at a density of $1.3\ \text{g cm}^{-3}$ (Bolch 1997). Single cysts were then transferred to Nunclon (Thermo Fisher Scientific, Hannover, Germany) $0.5\ \text{mL}$ microwells subjected to an irradiance of $100\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ and 24 h light, and filled with Erd-Schreiber medium (ESM) medium (Watanabe et al. 2000) at temperatures and salinities comparable to their respective natural environments

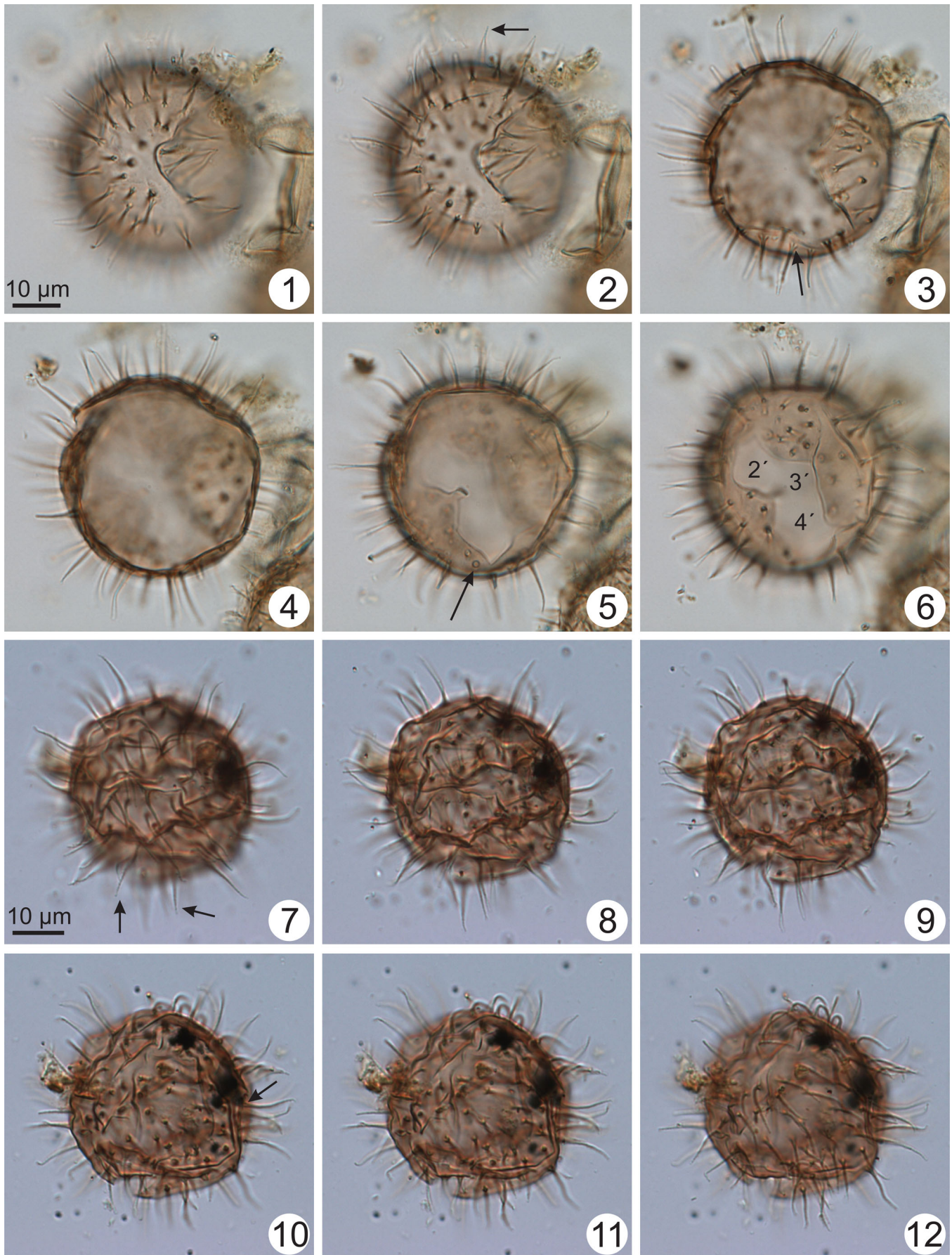


Plate 1. 1–12. *Islandinium pacificum* sp. nov. 1–6. holotype, Saanich Inlet, slide UVic 2009-661-1, EF V43/2 (label to the left), incrementally lowered focus; arrows indicate barbs on the processes (2), cavate process base (3) and circular cross section of process base (5). Interpreted tabulation of archeopyle is indicated (6). 7–12. Kuyquot Sound, Holocene, UVic 2015-643, incrementally lowering focus; arrows indicate barbs (7) and cavate process base (10).

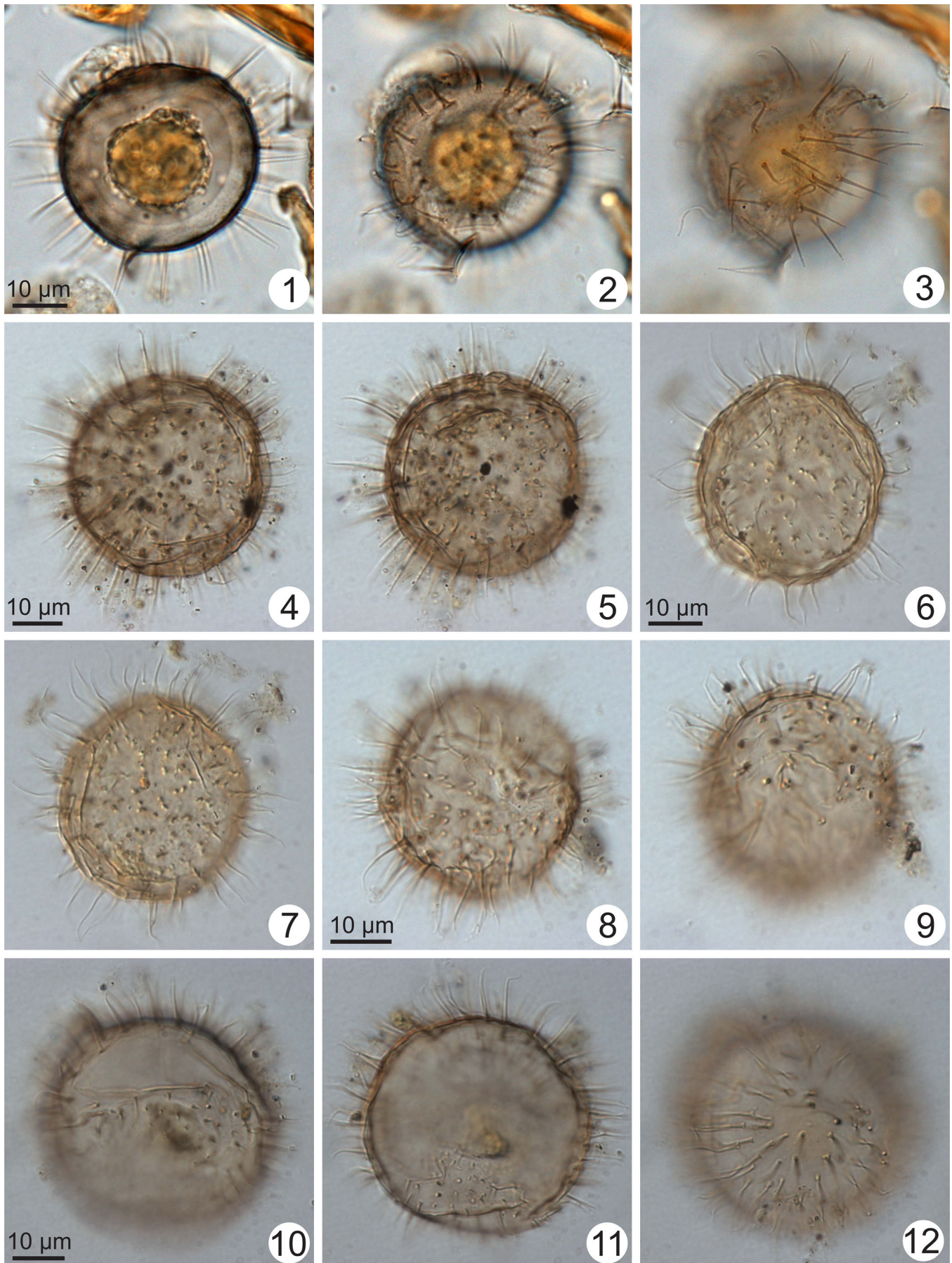
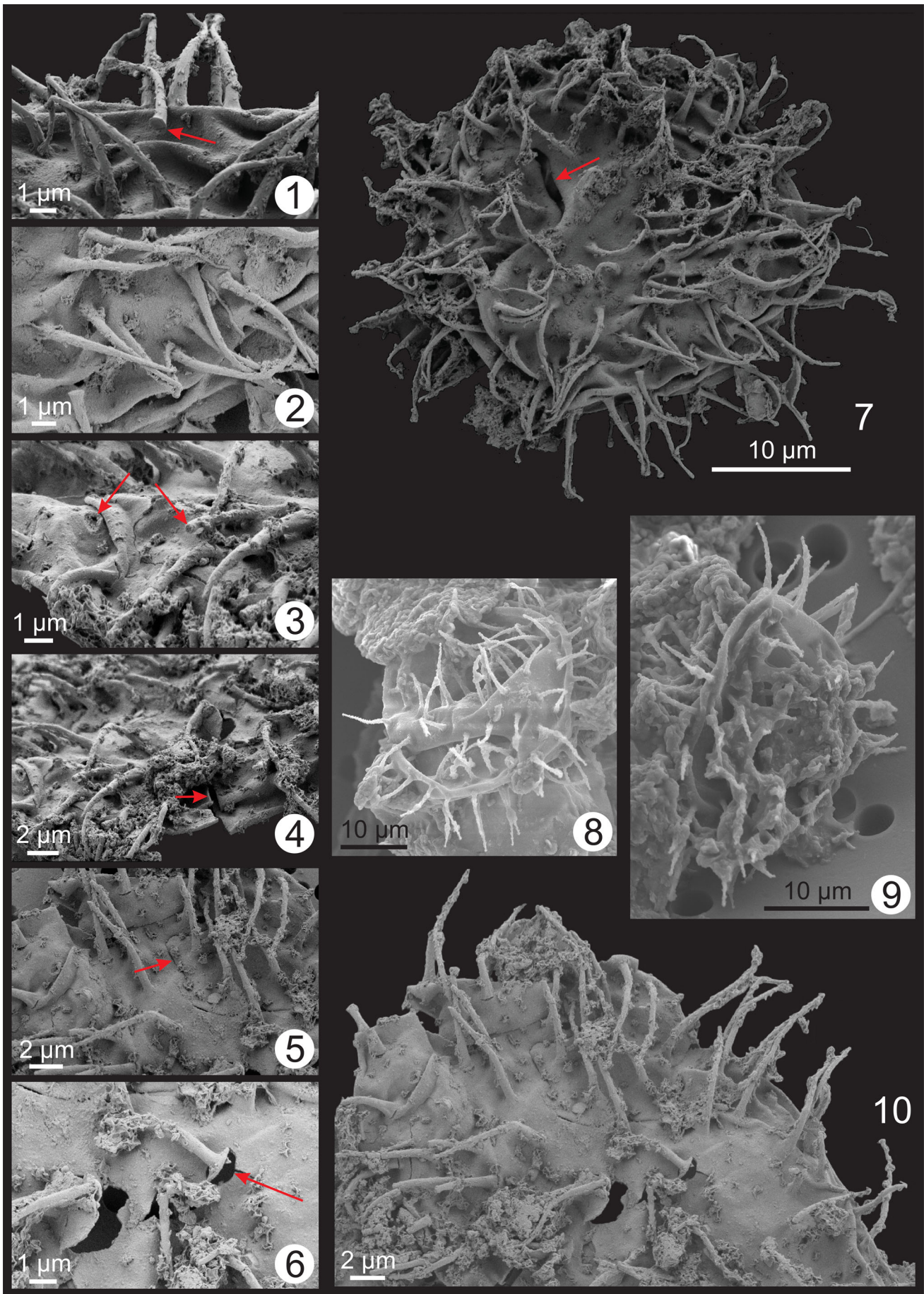


Plate 2. 1–12. *Islandinium pacificum* sp. nov. 1–3. Central Strait of Georgia, modern. 1. optical section, with endospore clearly visible; 2. intermediate focus, with archeopyle visible; 3. upper focus. 4–12. Eemian, Vøring Plateau. 4–5. 794.5 I 01e. 6–7. 810.5 II 07d. 8–9. 796.5 I 04b. 10–12. 794.5 I 06.



(Table S1). Cysts were regularly checked for germination, and observations were performed under an Olympus IX70 (Olympus, Tokyo, Japan) inverted light microscope. Encysted and excysted cysts and motile cells were photographed and measured using an Olympus BX51 (Olympus) light microscope with a Nikon digital sight DS-1L 1 module (Nikon, Tokyo, Japan) with 100 \times oil immersion objectives. For each motile cell, the length and width were measured. For each cyst, the longest and shortest body diameter and at least the three longest processes were measured. The theca was stained with calcofluor to improve tabulation visibility (Fritz and Triemer 1985).

3. Results

3.1. Systematic paleontology

Division DINOFLAGELLATA

Class DINOPHYCEAE (Bütschli, 1885) Fensome et al., 1993

Subclass PERIDINIPHYCIDAE Fensome et al., 1993

Order PERIDINIALES Haeckel, 1894

Family PROTOPERIDINIACEAE Balech, 1988

Subfamily PROTOPERIDINIOIDEAE Balech, 1988

Genus *Islandinium* Head et al., 2001 emend. Potvin et al., 2013

Type species. *Islandinium minutum* (Harland et al. 1980) Head et al., 2001 emend. Potvin et al. 2013.

Other species in this genus. *Islandinium brevispinosum* (Pospelova & Head 2002), *Islandinium? cezare* (Head et al. 2001). The species *Protoperidinium tricingulatum* was transferred to *Islandinium* by Potvin et al. (2013), but this is invalid (Williams et al. 2017).

Islandinium pacificum sp. nov.

Plates 1–4

Synonyms.

2008 Protoperidinoid cyst type A: Van Nieuwenhove et al.

2008 Protoperidinoid indet. cyst type A: Van Nieuwenhove, pl. 9, figs 7–12, pl. 10, figs 1–12.

2013 '*Echinidinium?* sp. A': Radi et al., p. 50, pl. 3, figs 9–12.

Holotype. Plate 1, figure 1–6; cyst from surface sediments in a palynological slide (UVic 2009-661-1, England Finder V43/2 (label to the left)).

Type locality. Saanich Inlet (48°35.475'N, 123°30.211'W; water depth 228 m; station C of Mertens et al. 2012a).

Repository. The holotype is deposited in the Royal Belgian Institute of Natural Sciences (RBINS, Brussels, Belgium), entry IRSNB b7154.

Material examined. Modern sediments from Saanich Inlet, the Strait of Georgia and Oak Bay (Saalish Sea); Holocene sediments from Kyuquot Sound (western Vancouver Island); Eemian sediments from the Vøring Plateau (North Atlantic).

Diagnosis. Light brown spherical spiny cyst; proximochorate to chorate; spherical smooth central body. Cyst wall shows no visible separation, except at the processes, which are numerous, long ($\sim 10\ \mu\text{m}$) and with random and non-tabular arrangement; erect or recurved; slender, acuminate and unbranched; circular cross-section over its length and apiculocavate. Process surface smooth, harpoon-like, bearing fine barbs directed toward the cyst center. Archeopyle apical and saphopylic, corresponding to three apical plates (2', 3' and 4'; type A3). Operculum adnate. No other traces of tabulation are reflected on the cyst.

Description. Cyst is light brown and often strongly folded when empty (Plate 1, figure 7–12). There is no visible separation of the thin ($< 0.2\ \mu\text{m}$), smooth wall, except at the hollow process bases. The wall is smooth only, not smooth to scabrate as suggested by Radi et al. (2013). The central body is ornamented with numerous erect (e.g. Plate 2, figure 3) or curved (e.g. Plate 1, figure 7–12) processes of 7.4 to 12.7 μm long (22 to 43% of central body diameter). The base of the processes is circular with a diameter of 0.7 μm (N=9). The cross-sections are circular along the length of a process. The processes taper distally to acuminate tips. The base of the process is hollow, with the length of the cavity being 1–2 μm , corresponding to about 15% of the total process length (Plate 1, Plate 2). SEM observations reveal the processes bear fine barbs that point in a proximal direction (Plate 3). In LM, the barbs are mostly observed as simple granules. Apart from the barbs, the processes are smooth (Plate 3). The distal barbs may be joined and give the appearance of a slight expansion of the process tips (Plate 3), which are in reality acuminate. The processes appear to be irregularly distributed and show no evidence of tabulation. Process bases are spaced 2.1 (2.8) 4.4 μm (N=19) apart for Eemian specimens, and 2.3 (3.4) 4.0 μm (N=6) apart for Holocene specimens. Density of processes is ~ 11 per $10 \times 10\ \mu\text{m}^2$.

The archeopyle suture is the only evidence of tabulation and is often not visible due to folding of the cyst. The archeopyle is saphopylic and is formed by the loss of three apical plates (type A3): 2', 3' and 4' (Plate 1, figure 6). The first apical plate projects into the archeopyle and the X-Po plates may remain attached (Plate 1, figure 5). Plate 4' forms the largest (right) part of the archeopyle, with plates 3' and 4' forming the smaller left side of the archeopyle (Plate 1, figure 5 and 6). Living cysts contain a thick endospore (Plate 2, figure 1).

Dimensions. The morphometry of *Islandinium pacificum* from the northeast Pacific and northeast Atlantic oceans is summarized in Table 2. Holotype: central body diameter 41.5 μm , process length 11.9 μm . Overall range: central body diameter 25.0 (35.6) 46.0 μm (N=51), process length 6.0 (10.5) 14.0 μm (N=43). Holocene and modern sediments from the northeast Pacific: central body diameter 28.9 (35.6) 42.2 μm , process length 7.4 (10.3) 12.7 μm (N=17). Eemian

←
Plate 3. 1–10: *Islandinium pacificum* sp. nov., scanning electron microscope images. 1–2, 7 and 3–6, 10. two specimens from the Eemian, Vøring Plateau (–823.5 m); 8–9. surface sediment, Saanich Inlet, Stn. 2. 3. Arrows show that process is hollow at basis (left) and solid more distally (right). 5. Arrow shows trace of archeopyle. 6. Arrow shows process torn off at the basis.

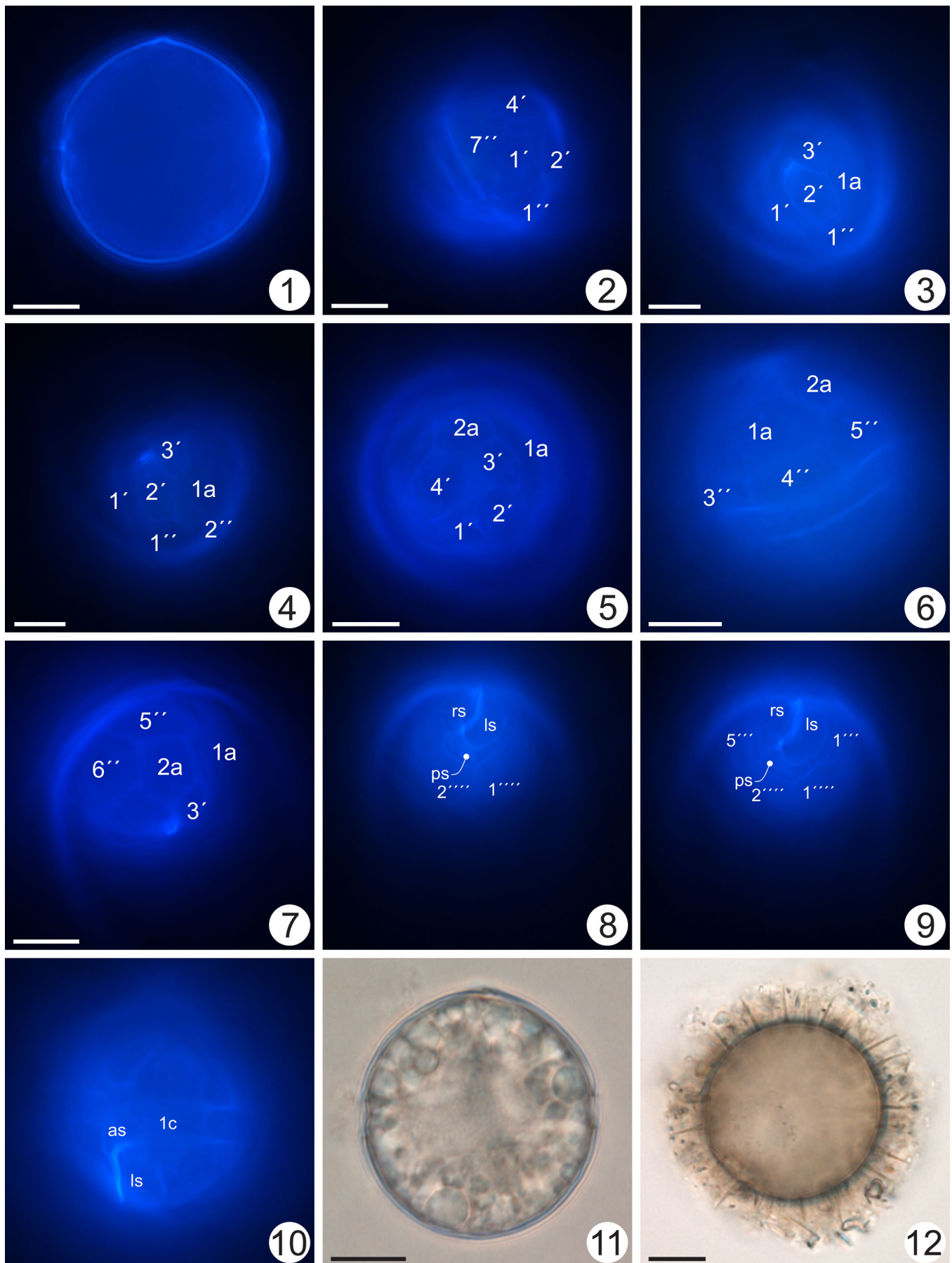


Plate 4. *Protoperidinium mutsuense* (1–11), after germination of an *Islandinium pacificum* cyst (12) from Saanich Inlet, Stn. 3. Theca stained with calcofluor (1–10) and LM (11–12). Interpreted tabulation is indicated. Scale bars: 10 μ m.

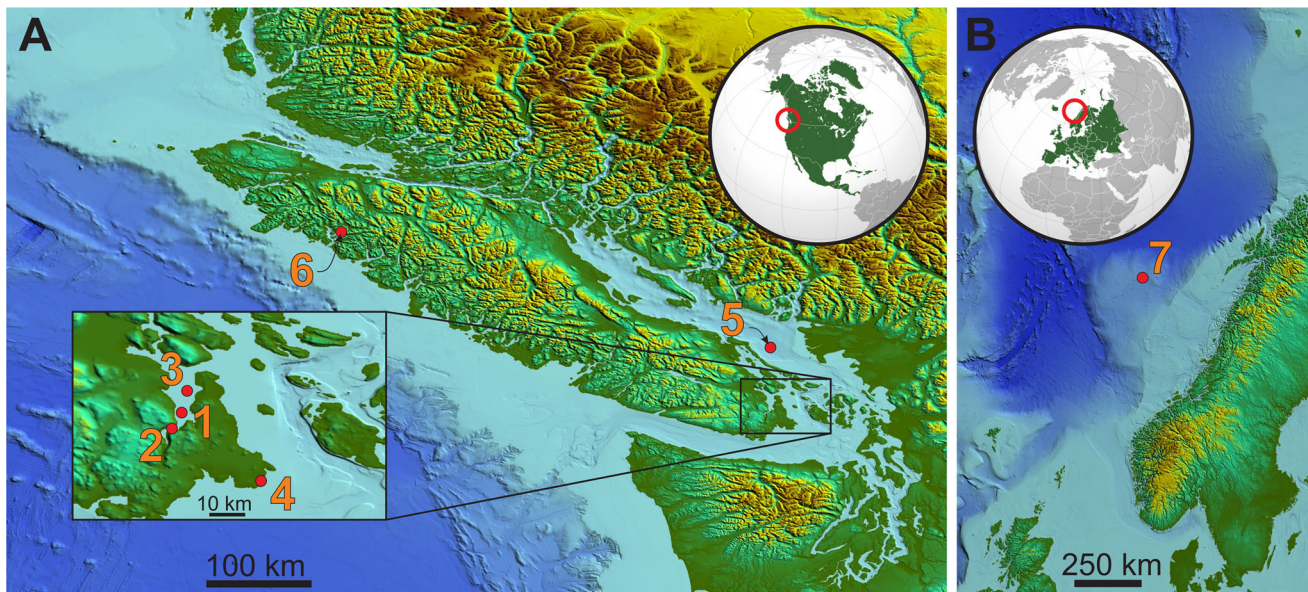


Figure 1. A–B, Locations studied in this paper. A, waters around Vancouver Island (British Columbia, Canada): Stn. 1–3: Saanich Inlet, Stn. 1 is in the central part of Saanich Inlet (station C from Mertens et al. 2012a), Stn. 3 is near Patricia Bay; Stn. 4 is in Oak Bay, Victoria; Stn. 5 is in the Strait of Georgia; Stn. 6 is in Kyuquot Sound. B, Stn. 7, on the Vøring Plateau offshore Norway. At 1–3 and 5, surface sediments were collected; 4 and 6 are core locations. See Table S1 for location details.

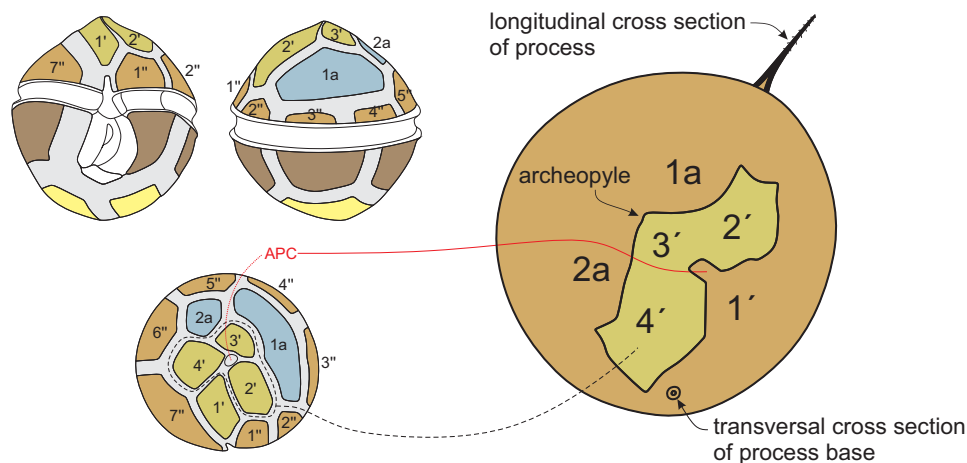


Figure 2. Schematic drawing of *Protoperidinium mutsuense*, after Abé (1936), with indication of epithecal tabulation (left), and of *Islandinium pacificum* sp. nov., with indication of the interpreted equivalent tabulation near the archeopyle (right). Nature of the processes is also illustrated. The drawing of *I. pacificum* was mirrored with respect to the holotype specimen (Plate 1), as the holotype shows the internal view of the archeopyle. APC, apical pore complex.

Table 2. Morphometrics of *Islandinium pacificum* sp. nov. from (a) Recent and Holocene sediments from the northeast Pacific Ocean, and (b) from the Eemian (MIS5e) from the Vøring Plateau, northeast Atlantic Ocean.

	Min.	Max.	Average	Median	SD	N
(a) Recent and Holocene NE Pacific						
Cyst body diameter (μm)	28.9	42.2	35.7	37.1	4.2	17
Process length (μm)	7.4	12.7	10.4	11.0	1.7	17
(b) Eemian N Atlantic						
Cyst body diameter (μm)	25.0	46.0	35.6	36.0	4.9	35
Process length (μm)	6.0	14.0	10.6	10.0	1.6	27

SD, standard deviation.

of the Vøring Plateau: central body diameter 25.0 (35.9) 46.0 μm (N = 35), process length 9.0 (10.8) 14.0 μm (N = 27).

Remarks. The cyst described as ‘Cyst type M1’ in Bringué et al. (2013, pl. 2, fig. 4) may be *Islandinium pacificum*, but barbs are not described or visible in the illustrations so this identification cannot be confirmed here.

Derivation of name. From the Pacific Ocean, where it occurs in modern sediments, and Holocene and uppermost Pleistocene sediments.

Motile stage. Cysts from Saanich Inlet hatched and the motile stage was identified as *Protoperidinium mutsuense* (Abé) Balech (Plate 4; see below).

Distribution and stratigraphic range. Eemian of the North Atlantic and uppermost Pleistocene and Holocene and modern sediments of the northeast Pacific.

3.2. Incubation experiments

3.2.1. Germination

Motile cells, here assigned to *Protoperidinium mutsuense*, emerged from *Islandinium pacificum* isolated from surface sediments of Oak Bay (Figure 1, station 4; four specimens identified), and the central part of Saanich Inlet (Figure 1, station 3; one specimen identified). After 1 or 2 days of incubation, motile cells germinated from the cysts. These cells died a few days after germination and never divided.

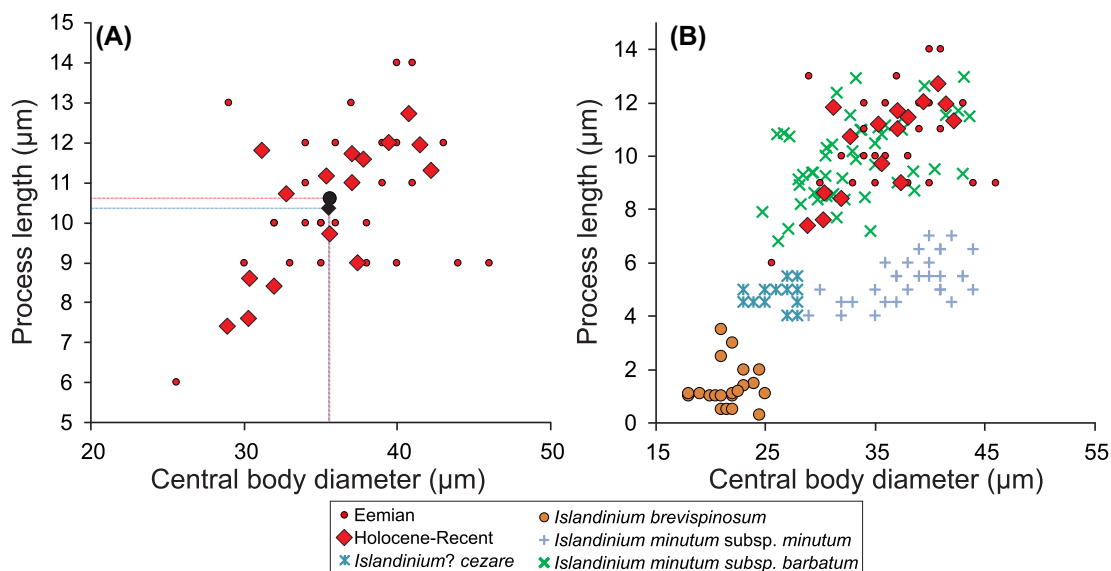


Figure 3. Graphical representation of *Islandinium pacificum* morphometrics: A, for the specimens from the Eemian of the North Atlantic and the Holocene of the North Pacific. Black points indicate respective averages. B, comparison with related species, with data from Head et al. (2001) for *Islandinium? cezare* and *Islandinium minutum* subsp. *minutum*; Pospelova and Head (2002) for *Islandinium brevispinosum*; and Potvin et al. (2017) for *Islandinium minutum* subsp. *barbatum*.

3.2.2. Morphology of the motile cell

The motile cells were subspherical, with a faintly pointed apex and without antapical projections (Plate 4, figure 1). The size of the motile cells was $33.5 \times 29.0 \mu\text{m}$ on average ($N=3$), with the epi- and hypotheca of roughly similar size. The cingulum shows no displacement, is very slightly excavated and is bordered by inconspicuous lists. Cells were thecate with a tabulation of Po, X, 4', 2a, 7'', 2c?, 4–5s?, 5''', 2'''' (Plate 4). On the epitheca, an apical pore complex (APC; Po and X) is clearly present and forms a short furrow (Plate 4, figure 4). The first apical plate (1') is asymmetric and orthogonal, contacting four major epithelial plates (2', 4', 1'' and 7'') and having minor contacts with the APC's X plate (Plate 4, figure 4 and 5) and the anterior sulcal plate (Plate 4, figure 2). There are two intercalary plates, with the left one (1a) elongated (Plate 4, figure 5) and the right one (2a) markedly smaller, equidimensional, and pentagonal (Plate 4, figure 7). The first intercalary plate (1a) has no contact with 1''. The first four precingular plates (1'', 2'', 3'' and 4'') are relatively small compared to the three last (5'', 6'' and 7''). The cingulum is probably formed by two cingular plates, with no intracingular sutures observed dorsally. A transitional plate is not observed (Plate 4, figure 10). The sulcal area is short, not extending to the center of the antapex (Plate 4, figure 8, 9), and is made up of four plates (or five, as the medial plate is hard to observe; Plate 4, figures 8 and 9). The anterior sulcal plate (as) is constricted in the middle, extends into the epitheca and touches plates 1', 1'' and 7'' (Plate 4, figure 10). All other sulcal plates are confined to the hypotheca. The left sulcal plate (ls) is J-shaped (Plate 4, figure 8) and indents the first postcingular plate (1'''; Plate 4, figure 9). The irregular hexagonal posterior sulcal plate (ps) has a pointed anterior end that is deflected to the right, in connection with the extension of the flagellar pore (Plate 4, figure 8, 9). A small flagellar fin on the left side of rs covers the pore (Plate 4, figure 8, 9). The plates have small, sparsely distributed pores (e.g. Plate 4, figure 8), except for the anterior sulcal plate (Plate 4, figure 10). These characteristics conform with

the description of *Protoperidinium mutsuense* as described by Abé (1936), except for the absence of a transitional plate.

4. Discussion

4.1. Comparison with other round brown process-bearing cyst species

The presence of barbs on the processes distinguishes *Islandinium pacificum* from other RBPCs except *Islandinium minutum*, specifically *I. minutum* subsp. *barbatum*. *Islandinium minutum* has a similar size range both in central body diameter and process length but can be distinguished from *I. pacificum* by its granular central body wall. Furthermore, the processes of *I. minutum* subsp. *minutum* have a microgranular surface (visible with SEM, Potvin et al. 2017) but rarely barbs. Processes of *Islandinium minutum* subsp. *barbatum* (Potvin et al. 2017), however, have conspicuous barbs, and distinction is to be made based on the faintly to prominently granular surface texture of the central body wall. *Islandinium cezare* differs by its characteristic expanded process terminations and its finely granular central body wall surface, and *I. brevispinosum* by its markedly shorter processes and the relatively small central body diameter (Figure 3B).

The saphopylic, polyplacoid archeopyle in *I. pacificum* distinguishes it from *Echinidinium* species, which have a chasmic archeopyle. Since the archeopyle is often not well visible in palynological preparations, size and process morphology can also be used (see Radi et al. 2013). *Echinidinium granulatum* differs from all *Islandinium* species in having a granular wall and granular processes instead of recurved barbs. Processes of *Echinidinium delicatum* are hollow over the entire length, and *Echinidinium aculeatum* has aculeate processes. Furthermore, these latter two *Echinidinium* species are smaller than *I. pacificum*. *Echinidinium karaense* also has a smooth central body wall surface and apiculocavate processes, but the processes are conical to tapering, slightly shorter and smooth, bearing no barbs.

Cysts of *Protoperidinium tricingulatum* have a theropylic archeopyle and capitate process terminations (Kawami et al. 2009). Cysts of *Protoperidinium lewisiae*, which also bear apiculocavate processes (Mertens et al. 2015), differ from *Islandinium pacificum* in having a theropylic archeopyle and being generally smaller while having more densely implanted processes. Furthermore, the tiny spinules on the processes of cysts of *P. lewisiae*, which might resemble barbs, are hard to observe using LM, whereas they are easily visible for *Islandinium pacificum* under LM. While having similar dimensions, cysts of *Niea acanthocysta* are different from *Islandinium pacificum* in having a microgranular wall and solid, often recurved processes (Mertens et al. 2015; Liu et al. 2015b).

4.2. Comparison of *Protoperidinium mutsuense* to other motile stages and classification

The tabulation of *Protoperidinium mutsuense*, identified here as the motile stage of *Islandinium pacificum*, fits with the definition of the genus *Islandinium* as described by Potvin et al. (2013), except for the number of cingular plates. It differs from the theca of *Islandinium minutum* (described by Potvin et al. 2013), however, in several ways. First, the shapes of the apical intercalary plates are different, and they are of dissimilar size. Second, the sulcal plates are different, particularly the shape of the as and ls plates. A further comparison with other comparable species such as *Archaeperidinium minutum* was made by Potvin et al. (2013).

Historically, *Protoperidinium mutsuense* has been classified in several ways. Abé (1981) and Balech (1974) accentuated different characters of the motile stage to classify the genus *Protoperidinium*. Balech (1974) emphasized the number of anterior intercalary plates, the shape of the second anterior intercalary (2a) plate (quadra, penta or hexa), the number of precingular plates and the shape of the first apical plate (1' ortho, meta or para) and the number of cingular plates. In contrast, Abé (1981) subdivided *Peridinium* (*Protoperidinium* and related species) into three subgenera (i.e. *Protoperidinium*, *Mesoperidinium* and *Veroperidinium*) based on the configuration and shape of the posterior sulcal (Sp) plate, and further subdivided these subgenera into groups. Abé (1936, 1981) thus placed *Protoperidinium mutsuense* in the *Monovela* group of the subgenus *Veroperidinium*. On the other hand, mainly due to the fact that there are two anterior intercalary plates, Balech (1974) related *P. mutsuense* to *Archaeperidinium*.

It is clear that *Protoperidinium mutsuense* does not belong to the genus *Archaeperidinium*: *Protoperidinium mutsuense* differs in morphology from the genus *Archaeperidinium* in the thecate shape, the absence of a pronounced apical horn, and the absence of a transitional plate and its cyst morphology (Yamaguchi et al. 2011; Mertens et al. 2012b). *Protoperidinium mutsuense* can be classified within the *Monovela* group as defined by Matsuoka and Kawami (2013) which is subdivided into several subclades. The *Americanum* subclade includes, among others, *Islandinium*; the *Minutum*

subclade includes *Archaeperidinium*; the *Monovelum* subclade includes, among others, *Echinidinium* (Potvin et al. 2017).

Similar to *Islandinium minutum*, *I. pacificum*, as described here, belongs to the *Americanum* subclade, which further includes *Protoperidinium americanum*, *P. tricingulatum*, *P. parthenopes*, *P. fusiforme*, *P. fukuyoi* and *P. haizhouense* (Matsuoka and Kawami 2013; Potvin et al. 2017). More specifically, the tabulation pattern of *Protoperidinium mutsuense* largely fits into the variability of the thecal arrangement of these species in this subclade, which can be summarized as Po, X, 2–4a, 6–7'', 3–4c, 5–7s, 5''', 2'''' (Liu et al. 2013; Matsuoka and Kawami 2013). The possible discrepancy in the cingular plate number needs further investigation. The three-plate apical archeopyle further justifies that *Islandinium pacificum* (*Protoperidinium mutsuense*) belongs to the *Americanum* subclade of the *Monovela* clade. Molecular (large and small subunit rDNA) data of *Protoperidinium mutsuense* are needed to reveal the exact phylogenetic relation with the available sequences and the placement within the protoperidinioid clade.

4.3. Occurrence and paleoecology

Islandinium pacificum sp. nov. is described here from surface sediments from the northeast Pacific Ocean, mainly the Vancouver Island fjords, Saanich Inlet and the Strait of Georgia (Figure 1A). Average SSTs in the Strait of Georgia are 6–7 °C in winter and 13–16 °C in summer (Pospelova et al. 2010), and they are comparable in Saanich Inlet (Price and Pospelova 2011) and the Vancouver Island fjords (Gurdebeke et al. 2018). SSS varies between 20 and 32 in these waters (Pospelova et al. 2010; Price and Pospelova 2011; Gurdebeke et al. 2018). The species was also frequently encountered in a Holocene record from Kyuquot Sound (Vancouver Island), from 7.5 ka BP onward (Gurdebeke et al. unpub. data). During this interval, *I. pacificum* reaches concentrations up to ~1500 cysts g⁻¹ (475 cysts g⁻¹ on average), corresponding to a maximum of 2.2% of the assemblage. Farther south, in the Santa Barbara Basin (off the California coast), Pospelova et al. (2006) documented these cysts from ~23 ka BP onward and Bingué et al. (2013) reported a similar form in a sediment trap samples from the same basin. The species described here has been observed in last interglacial (Eemian) deposits from the Vøring Plateau, Norwegian Sea, reaching up to 3% of the assemblages (Van Nieuwenhove et al. 2008, 2011), where its occurrence is possibly related to slightly freshened surface waters (salinity 33 to 34 based on transfer function reconstructions; Van Nieuwenhove and Bauch 2008) and pronounced seasonality. Though Head et al. (2001) characterized species in the genus *Islandinium* as indicative of a low-temperature environment, subsequent new species descriptions broadened the ecological range of this genus to temperate waters (Pospelova and Head 2002), which is in line with the results reported here for *I. pacificum* sp. nov.

5. Conclusions

The new dinoflagellate cyst *Islandinium pacificum* sp. nov. is described here from modern sediments from Saanich Inlet,

with further observations from Holocene and surface sediments from Vancouver Island and Eemian sediments from the North Atlantic. Morphologically, *Islandinium pacificum* sp. nov. is most similar to *Islandinium minutum* subsp. *barbatum*, from which it is distinguished by its smooth wall. Incubation experiments revealed that the motile stage for *Islandinium pacificum* sp. nov. is *Protoperidinium mutsuense*. The species occurs in the uppermost Pleistocene, Holocene and modern sediments of the temperate zones of the northeast Pacific Ocean, and during the last interglacial also in the northern North Atlantic Ocean.

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