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ISLANDINIUM BREVISPINOSUM SP. NOV. (DINOFLAGELLATA), A NEW ORGANIC-WALLED DINOFLAGELLATE CYST FROM MODERN ESTUARINE SEDIMENTS OF NEW ENGLAND (USA)[1]

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Modern estuarine environments remain underexplored for dinoflagellate cysts, despite a rapidly increasing knowledge of cyst distributions in open marine sediments. A study of modern estuarine sediments in New England has revealed the presence of *Islandinium brevispinosum* sp. nov., a new organic-walled dinoflagellate cyst that is locally common and probably of heterotrophic affinity. Resistance of this cyst to standard palynological processing indicates its geological preservability, although fossils are not yet known. Previously assigned species of the genus *Islandinium* are characteristic of polar and subpolar environments today and cold paleoenvironments in the Quaternary. The present record of *I. brevispinosum* extends the ecological and geographical range of this genus into the warm temperate zone, where *I. brevispinosum* occupies specific environments with reduced salinities and elevated nutrient levels.

Key index words: **Atlantic Ocean; estuaries; *Islandinium brevispinosum*; modern sediments; Massachusetts; nutrients; organic-walled dinoflagellate cysts; Rhode Island; salinity; USA**

Dinoflagellate cysts are being studied increasingly in modern marine systems where they reflect environmental conditions with considerable sensitivity. Northern North Atlantic and Arctic cyst distributions are now well documented (Rochon et al. 1999, de Vernal et al. 2001) and provide the basis for detailed quantitative reconstructions of the Quaternary oceanic record in this region (e.g. de Vernal et al. 1996, 2000, de Vernal and Hillaire-Marcel 2000, Hillaire-Marcel et al. 2001). In contrast to the open ocean, coastal waters adjoining the North Atlantic have a more variable hydrography, and the mapping of cyst distributions is therefore more complex. The distribution of cysts in these coastal regions is not well known, estuarine systems being generally underexplored for dinoflagellate cysts. Of the few studies that have focused solely on North American estuaries, most have been conducted along the Canadian Atlantic coast (Mudie and Short 1985, de Vernal and Giroux 1991). Dinoflagellate cysts from the temperate zone of the east coast of the United States have been studied either in low detail (Wall et al. 1977, Dale 1996) or to describe the biogeographical distribution of selected toxic species (Anderson et al. 1994, Anderson 1998). Comprehensive surveys have not been undertaken previously.

This report is part of a larger investigation to map and explain the distribution of dinoflagellate cysts from selected environments along the New England (northeastern United States) coastline. Well-preserved material has been investigated from surface and core sediments that represent less than 500 years of deposition. Localities studied include several embayments of Buzzards Bay, New Bedford Harbor, Clarks Cove, Apponagansett Bay, Waquoit Bay, Jehu Pond, Narragansett Bay, and coastal lagoons of Rhode Island (Fig. 1). The present paper describes *Islandinium brevispinosum* sp. nov., a locally common component of dinoflagellate cyst assemblages in modern estuarine sediments of New England where it is particularly associated with nutrient rich waters.

Islandinium is a recently proposed protoperidiniacean cyst genus (Head et al. 2001) that accommodates round brown spiny cysts with an apical archeopyle. This genus until now comprised only *I. minutum* (Harland and Reid in Harland et al. 1980) Head et al., 2001 and *I. cezare* (de Vernal et al. 1989 ex de Vernal in Rochon et al. 1999) Head et al., 2001. Both species are known principally from modern high-latitude sediments and from cold-climate Quaternary deposits. Our record of *I. brevispinosum* sp. nov. unequivocally extends the ecological range of this genus into warm temperate waters. We provide a formal description of this cyst species and discuss its ecological significance.

MATERIALS AND METHODS

Samples. Samples were collected from three embayments in Buzzards Bay (New Bedford Harbor, Apponagansett Bay, and Clarks Cove), in Waquoit Bay and adjacent Jehu Pond (MA), in

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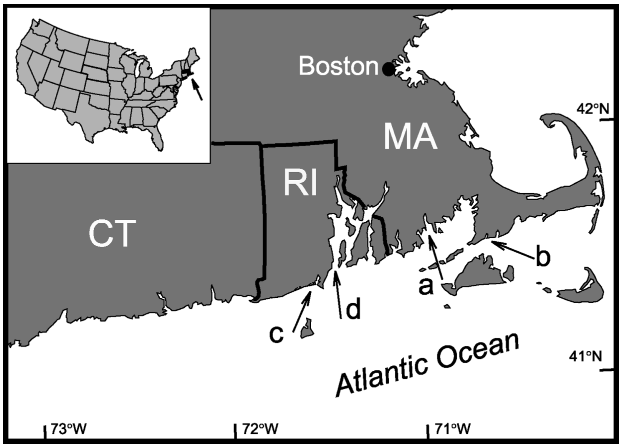


FIG. 1. Location of New England sites where *Islandinium brevispinosum* sp. nov. has been found. *Islandinium brevispinosum* is reported from modern sediments of (a) Apponagansett Bay, Clarks Cove, New Bedford Harbor; (b) Waquoit Bay and Jehu Pond (Massachusetts, USA); (c) coastal lagoons of Rhode Island (USA); and (d) Narragansett Bay.

eight back-barrier coastal lagoons of Rhode Island, and in the central part of Narragansett Bay (RI) (Figs. 1 and 2). Sediments analyzed were generally fine sands, silt, and mud from surface and core sediments.

Surface sediments from New Bedford Harbor, Apponagansett Bay, Clarks Cove, Waquoit Bay, Jehu Pond, and coastal lagoons of Rhode Island were collected by a grab corer deployed from a boat or by hand using a mini-piston corer while snorkeling. The top 2 cm were retained, and we assume they represent less than 10-year deposition in these generally rapidly accreting systems (Boothroyd et al. 1985, Pospelova, unpublished data). Sediments taken from experimental tanks at the Marine Environmental Research Laboratory (University of Rhode Island) had originated as surface sediment from the central part of Narragansett Bay before their transfer to the experimental tanks (see Keller et al. 1999 for details).

In addition to surface sediments, three sediment cores were collected from New Bedford Harbor and Apponagansett Bay and represent less than 500 years of deposition (Pospelova et al. 2002). These cores were collected either by pressing a core liner into the sediments (hand corer) or by using a gravity coring device (Benthos Model 2171, Benthos, Inc., North Falmouth, MA, USA). Upon collection, all the sediments were immediately transported to the laboratory and stored at 4° C in the dark until processing.

Methods. Sediment samples of known volume were first dried at 40° C and then treated with cold 10% HCl for 2 min to remove calcium carbonate particles. Material was then rinsed twice with distilled water and sieved through 125 μm and retained on 10-μm mesh to eliminate coarse and fine material. To dissolve siliceous particles, most of the samples were treated in a hot water bath with 40% hydrofluoric acid for 20 min and 10 min with cold HCl to remove fluorosilicates. Subsequently, the residue was rinsed twice with distilled water, sonicated for between 30 s and 2 min, and finally collected on a 10-μm mesh sieve, having been centrifuged between each step. Aliquots of residue (one or two drops) were mounted on microscope slides with glycerine jelly, and dinoflagellate cysts were studied under a light microscope (63× and 100× objectives). Illustrations were made using a Leica DML-RB microscope and DC3 digital camera (Leica Microsystems, Wetzlar GmbH, Wetzlar, Germany). For SEM, residues were suspended in deionized water and placed on coverslips to dry. The mounted coverslips were then sputter coated with gold and platinum and searched under Hitachi (S-2300) SEM (Hitachi, Ltd., Tokyo, Japan) for cysts of *I. brevispinosum.*

Repository. All figured material photographed under light microscopy is deposited in the type collection of the British Geological Survey (Keyworth, UK) under the accession numbers MPK 12549–12553. All remaining microscope slides and residues are stored in the Paleoenvironmental Laboratory, McGill University, Canada.

RESULTS

Islandinium brevispinosum Pospelova et Head sp. nov.

Division: Dinoflagellata (Bütschli 1885) Fensome et al., 1993
Subdivision: Dinokaryota Fensome et al., 1993
Class: Dinophyceae Pascher, 1914
Subclass: Peridiniphycidae Fensome et al., 1993
Order: Peridiniales Haeckel, 1894
Suborder: Peridiniineae (Autonym)
Family: Protoperidiniaceae Balech, 1988
Subfamily: Protoperidinioideae Balech, 1988
Genus: *Islandinium* Head et al., 2001
Species: *Islandinium brevispinosum* Pospelova et Head sp. nov.

Diagnosis. Cystae parvae, proximae vel proximochoratae cum copore in medio globali vel subglobali. Murus fuscus vel fulvus colore; superficies levis tecta solidis spinulis. Spinula, fere similes longitudine figuraque, fastigata ad cacumines acres vel hebetes, nontabulare distribuuntur. Archeopyla saphopylica formata est laminis apicalibus secundis, tertiis et quartis separate amissis; tertia apicalis lamina fere aequalis circum dorsoventralem lineam mediam. Suturae archeopylae adiectae praeterea adsint; alioqui nullum indicium clarum tabulationis.

Small proximate to proximochorate cysts with spherical to subspherical central body. Wall is brown to pale brown in color; surface smooth and covered with numerous solid spinules. Spinules more or less similar in length and shape, taper to sharp or blunt tips, and have nontabular distribution. Archeopyle saphopylic, formed by separate loss of the second, third and fourth apical plates; third apical plate approximately symmetrical about the dorsoventral midline. Accessory archeopyle sutures may also be present; otherwise no clear indication of tabulation.

Etymology: Latin *brevis* short, small; and *spinosus* thorny. With reference to the small spines that characterize this species.

Holotype: Sample NBH-324 slide 7, England Finder reference S30/3 (label to left); specimen MPK 12549; Figure 3, a–m. Modern sediment from New Bedford Harbor, Atlantic coast of Massachusetts (USA).

Description: Cysts brown to pale brown in color. Central body spherical to subspherical, with smooth surface under light microscopy and SEM, and wall thickness of about 0.3 μm or less, appearing unstratified under light microscopy. Surface bears numerous, solid, nontabulate, closely but irregularly distributed spinules with basal diameter of approximately 0.3 μm. Adjacent spinules usually separated at base by about 1.0 μm, but some basal fusion occurs in some specimens; density of spinule distribution varies somewhat

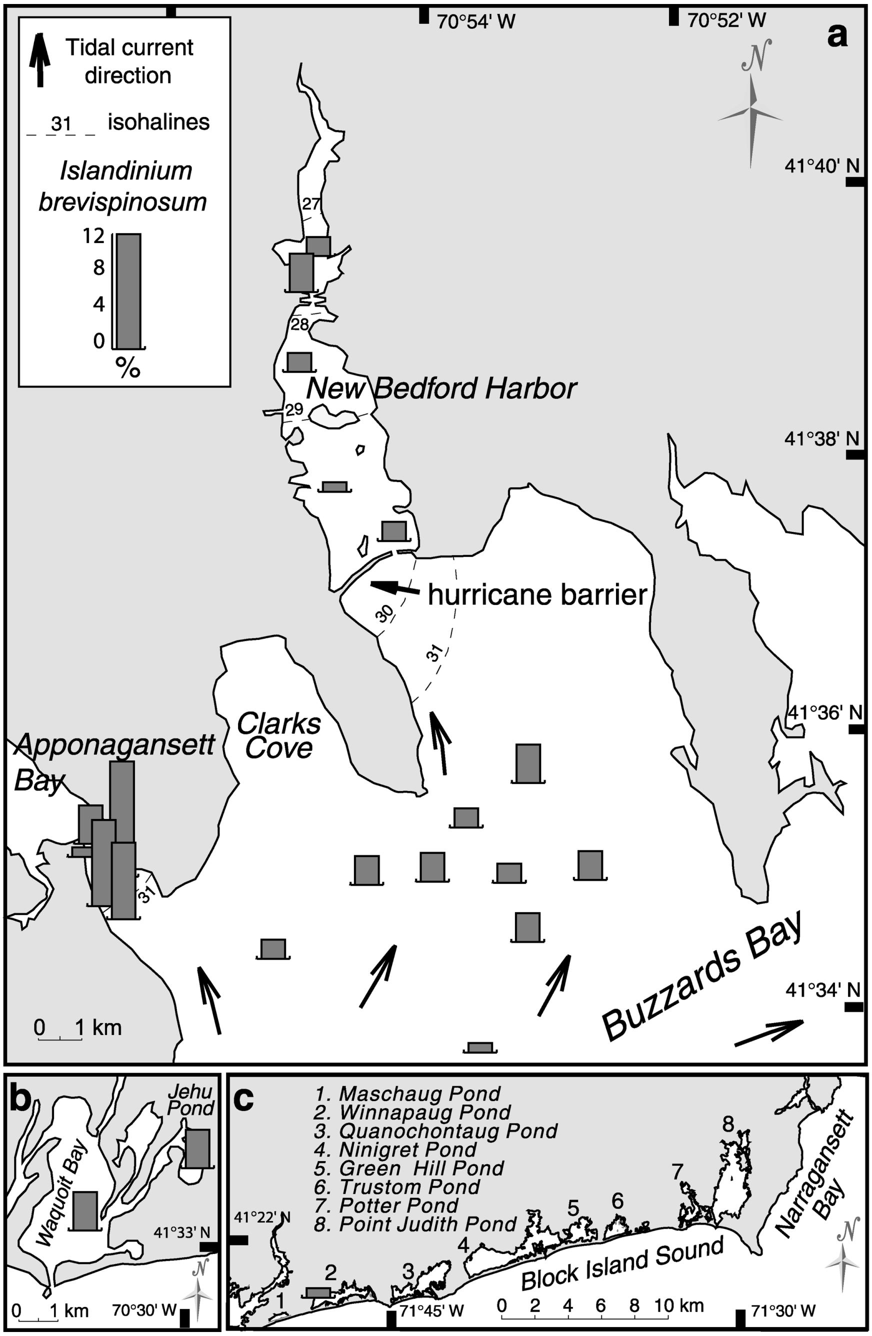
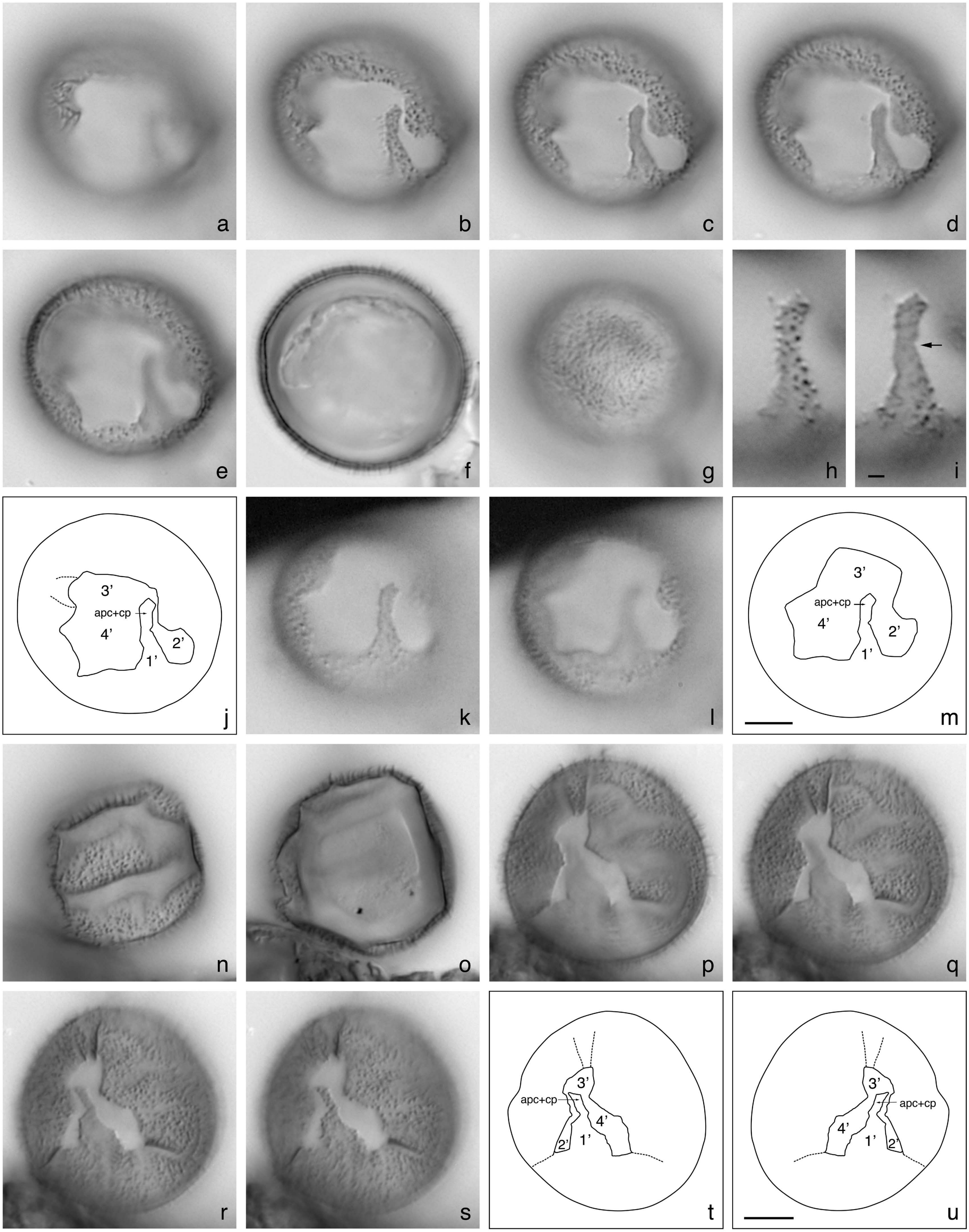


FIG. 2. Map of the spatial distribution and relative abundance of *Islandinium brevispinosum* sp. nov. in New England estuaries: (a) Apponagansett Bay, Clarks Cove, and New Bedford Harbor (MA); (b) Waquoit Bay and Jehu Pond (MA); (c) coastal lagoons of Rhode Island.

between and within individual specimens. Length of spinules varies from 0.3 μm where they may appear as small bumps, up to 3.5 μm where they may be curved. Spinule length fairly constant for individual specimens; ranges from 1% to 14% of body diameter, averaging 5%. Spinules taper to fine or blunt points, as observed under both light (Figs. 3–4) and SEM (Fig. 5). Archeopyle is saphopylic, formed by separate loss of the three apical plates 2′, 3′, and 4′. Canal plate (and presumably apical pore complex) remains attached to first apical plate (1′) (Fig. 3, a–u, and possibly Fig. 4, i–m) or is lost during archeopyle formation (Fig. 4, a–h, n–p). Boundary between canal plate and 1′ is marked by a notch in archeopyle outline (Fig. 3i). Plates 3′ and 4′ are approximately the same size, whereas plate 2′ might be slightly smaller. Archeopyle, including position of third apical plate, broadly symmetrical about dorsoventral midline. Cysts show no epifluorescence.

Measurements: Holotype: central body diameter 22 μm; average length of process 1.0 μm. Range: central body diameter 18(21.5)25 μm (standard deviation 1.8 μm); average process length: 0.3(1.1)3.0 μm (standard deviation 0.6 μm). Twenty-nine specimens were measured. See also Figure 7.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Discussion: The archeopyle was seldom seen clearly in the 315 specimens scrutinized during the present study, largely due to the very thin cyst wall which readily collapses and folds. The holotype has a clearly visible archeopyle and was inflated when freshly mounted and examined in Montreal (Fig. 3, k–m). It had become slightly distorted upon its arrival in Cambridge, although all major features remain clearly discernible (Fig. 3, a–j). The archeopyle and interpreted position of adjoining plate boundaries is given in Figure 6a. These boundaries, including the presumed orthostyle first apical plate, are conjectural because accessory archeopyle sutures were seldom observed. The paucity of accessory archeopyle sutures, along with a lack of information on the number of intercalary plates, prevents full determination of the episomal tabulation. However, on the basis that *I. brevispinosum* probably represents the cyst of a species of the genus *Protoperidinium* Bergh 1881, two possibilities are preferred. The first assumes the presence of three intercalary plates (Fig. 6b), which is a common feature of *Protoperidinium* species having a symmetrical episomal tabulation. The archeopyle in *I. brevispinosum* is relatively symmetrical about the dorsoventral midline, particularly regarding the position of the third apical plate, implying (but not proving) a symmetrical episomal tabulation. The second less likely possibility (Fig. 6c) is of four intercalary plates. Although a highly unusual configuration within the genus *Protoperidinium*, this possibility is due to a strong similarity between the archeopyles of *Islandinium brevispinosum* and of the cyst of *Protoperidinium americanum* (Gran and Braarud 1935) Balech 1974 (Lewis and Dodge 1987; Fig. 6g). Not only does *Protoperidinium americanum* have four intercalary plates (Fig. 6h), it is also the only motile-defined species within the genus *Protoperidinium* whose cyst is known to have an apical archeopyle. Hence, based on the above considerations, we favor three or perhaps even four intercalary plates for *I. brevispinosum*.

Comparison: Islandinium brevispinosum closely resembles *Islandinium minutum* (Harland and Reid in Harland et al. 1980) Head et al., 2001 described from modern sediments of the Beaufort Sea, Canadian Arctic. However, *I. minutum* is larger (central body maximum diameter 29–50 μm; average process length 3.5–7.0 μm; Head et al. 2001) and has a granulate wall surface compared to the smooth wall surface of *I. brevispinosum*. Statistical analysis of average process length versus central body diameter for *I. brevispinosum* and *I. minutum* demonstrates two separate clusters in the distribution (Fig. 7). The archeopyle of *I. brevispinosum* differs from that of *I. minutum* in its greater symmetry: plate 3′ is offset strongly to the left on *I. minutum* (Fig. 6, d–f) and implies a different configuration of intercalary plates (Fig. 6, e and f). Also, plate 2′ appears to be pentagonal in *I. brevispinosum*, whereas it is more or less quadrangular in *I. minutum*.

Islandinium cezare (de Vernal et al. 1989 ex de Vernal in Rochon et al. 1999) Head et al., 2001, described from late glacial sediments of Québec, differs from *I. brevispinosum* in its larger size, granulate wall surface, and in having long processes with expanded process tips.

The cyst of *Protoperidinium americanum* differs in its larger size (diameter 34–52 μm), prominent wall layering, and absence of processes (Lewis and Dodge 1987; Fig. 6g). Its archeopyle is relatively smaller than that of *I. brevispinosum*, although similar in shape.

Occurrence: Islandinium brevispinosum has been found only in modern (between <500 and <10 year) estuarine sediments of New Bedford Harbor, Clarks Cove, Apponagansett Bay, Waquoit Bay and Jehu Pond (Atlantic coast of Massachusetts, USA), Winnapaug Pond, and Narragansett Bay (Rhode Island, USA) (Fig. 2). The highest abundance (12%) is found in nutrient rich waters characterized by 23° C mean summer temperature and 30 psu mean summer salinity. Distribution is presumably more widespread than presently described. Cell contents occur in some cysts including the holotype, indicating that this is an extant species.

Thecal affinity: As with *I. minutum*, an affinity with the subfamily Protoperidinioideae is indicated from the epicystal tabulation and overall morphology of the cyst (Head et al. 2001). The brown cyst wall coloration and lack of epifluorescence suggest a species whose motile stage has a heterotrophic feeding strategy, which is predominant in the Protoperidiniaceae. Because the cysts are extant, the motile stage must be present in the water column. However, the only species of *Protoperidinium* presently reported for Buzzards Bay (New Bedford Harbor, Apponagansett Bay, and Clarks Cove) are *P. bipes* (Paulsen 1904) Balech 1974, *P. claudicans* (Paulsen 1907) Balech 1974, *P. pellucidum* Bergh 1881, and *P. steinii* (Jörgensen 1900) Balech 1974 (see Pierce and Turner 1994). Of these, *P. claudicans* is known to produce a cyst morphologically different from *I. brevispinosum* (Head 1996), *P. bipes*

FIG. 3. *Islandinium brevispinosum* sp. nov. Photomicrographs are interference contrast images. (a–m) Holotype from modern sediments of New Bedford Harbor, Massachusetts (USA), NBH-324/7, S30/3, MPK 12549, central body max. diameter 22 μm; apical view of specimen in present (a–j) and original (k–m) condition. (a–g) Upper surface with archeopyle and successively lower foci to antapical surface, with f showing cell contents. (h, i) Magnified view of upper (h) and lower (i) surfaces of plate 1′, showing notch (marked by an arrow) indicating the interpreted border between plate 1′ and the canal plate. (j, m) Tracings of holotype in present (j) and original (m) condition. Scale bar represents 5 μm for a–g, j–m and 1 μm for h, i. (n–u) Paratype from modern sediments of Apponagansett Bay, Massachusetts (USA), sample AB-4/1, S62 1/2, MPK 12550, central body diameter 21 μm. (n–s) Antapical view of antapical surface and successively lower foci to apical surface with archeopyle; and (t, u) tracings of paratype where u is a reversed image of t to compare with holotype. Scale bar, 5 μm. (j, m, t, u) Tracings show principal archeopyle suture (solid line), folds (dashed line), and interpreted tabulation. Designations cp and apc represent the canal plate and apical pore complex, the latter being presumed present but not identified with certainty.

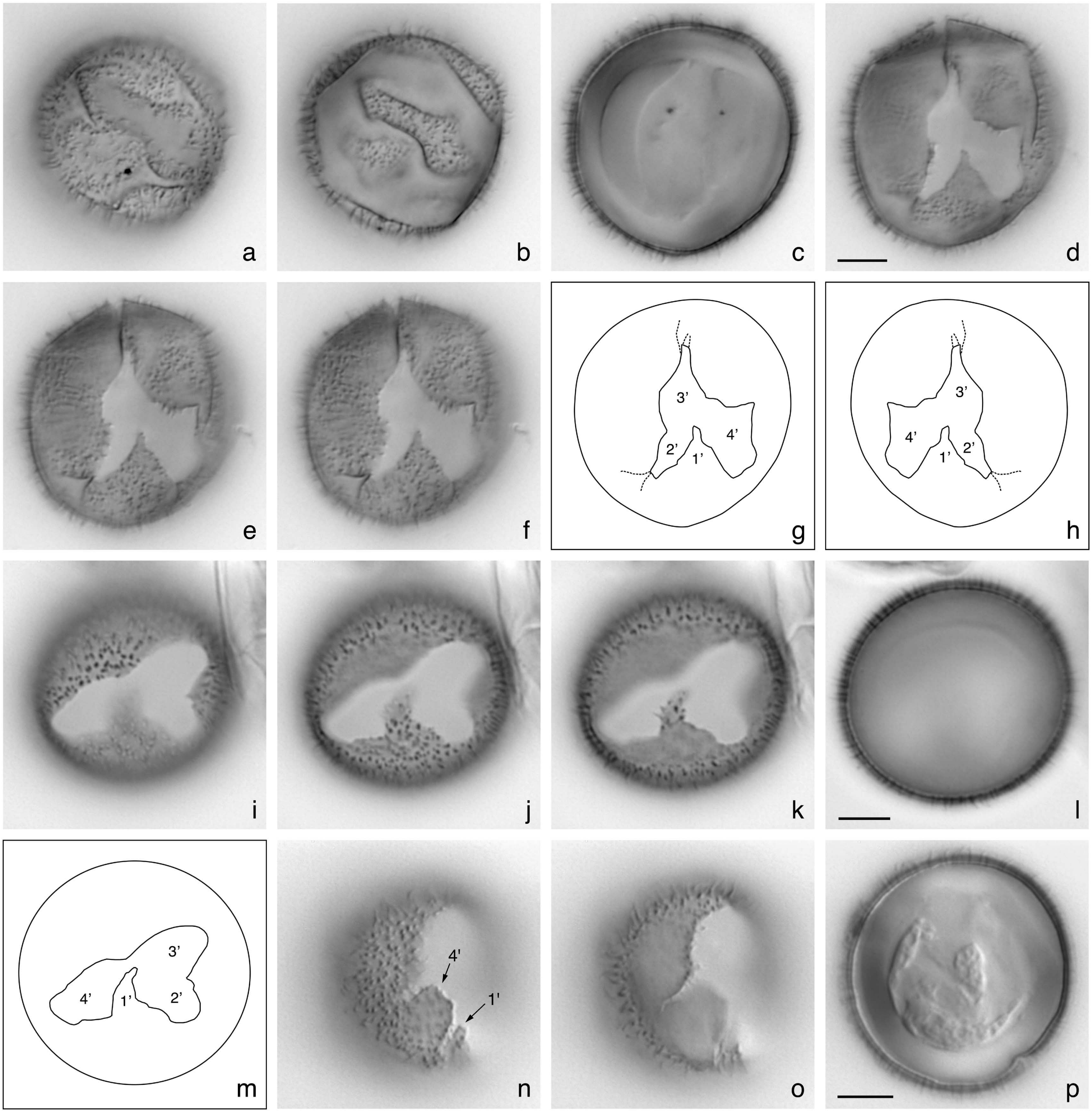

FIG. 4. *Islandinium brevispinosum* sp. nov. Photomicrographs are interference contrast (a–f, n–p) or bright field (i–l) images. (a–h) Specimen from modern sediments of New Bedford Harbor, Massachusetts (USA), sample NBH-324/2, R28/2, MPK 12551, central body diameter 24 μm. (a–f) Antapical view of antapical surface and successively lower foci to apical surface with archeopyle, and (g, h) tracings of specimen where h is a reversed image of g to compare with holotype. The three apical plates and canal plate are all lost from this specimen. Scale bar, 5 μm. (i–m) Specimen from modern sediments of Apponagansett Bay, Massachusetts (USA), sample AB-4/21, S46/0, MPK 12552, central body diameter 23 μm. (i–l) Apical view of apical surface with archeopyle and successively lower foci to mid-focus, and (m) tracing of specimen. Scale bar, 5 μm. (n–p) Specimen from modern sediments of New Bedford Harbor, Massachusetts (USA), sample NBH-324/xx, H27/1, MPK 12553, central body diameter 21 μm. Apical view of (n) apical surface showing release of plates 2′, 3′, and canal plate, but 4′ still adherent, (o) slightly lower focus, and (p) mid-focus showing protoplasm within cyst. Scale bar, 5 μm.

has a strongly asymmetrical episomal tabulation, and *P. pellucidum* and *P. steinii* are both probably too large to produce a cyst consistently as small as *I. brevispinosum.* No attempt to germinate *I. brevispinosum* has yet been made, but this approach will ultimately establish the thecal affinity of this cyst species.

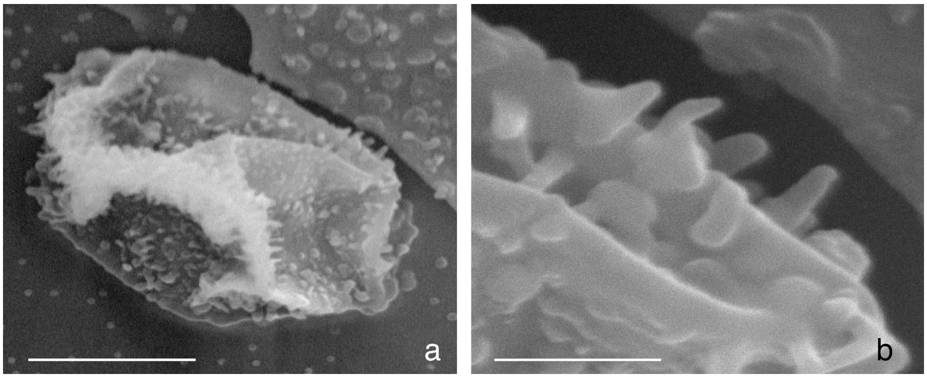

FIG. 5. *Islandinium brevispinosum* sp. nov. SEM images of specimen from modern sediments of Apponagansett Bay, Massachusetts (USA), sample AB-4. (a) Portrait showing process distribution. (b) High magnification view of a showing smooth wall surface and spinules tapering to blunt points. Scale bars, 10 μm (a) or 2 μm (b).

ECOLOGICAL DISTRIBUTION

A total of 315 complete and fragmented specimens of *I. brevispinosum* was observed in 54 sediment samples. All studied sites are characterized by shallow water in which depth ranges from 1 to 12 m. Embayments of Buzzards Bay were studied in most detail, with the analysis of 19 surface sediment samples (Pospelova, unpublished data) and 31 sediment sam-

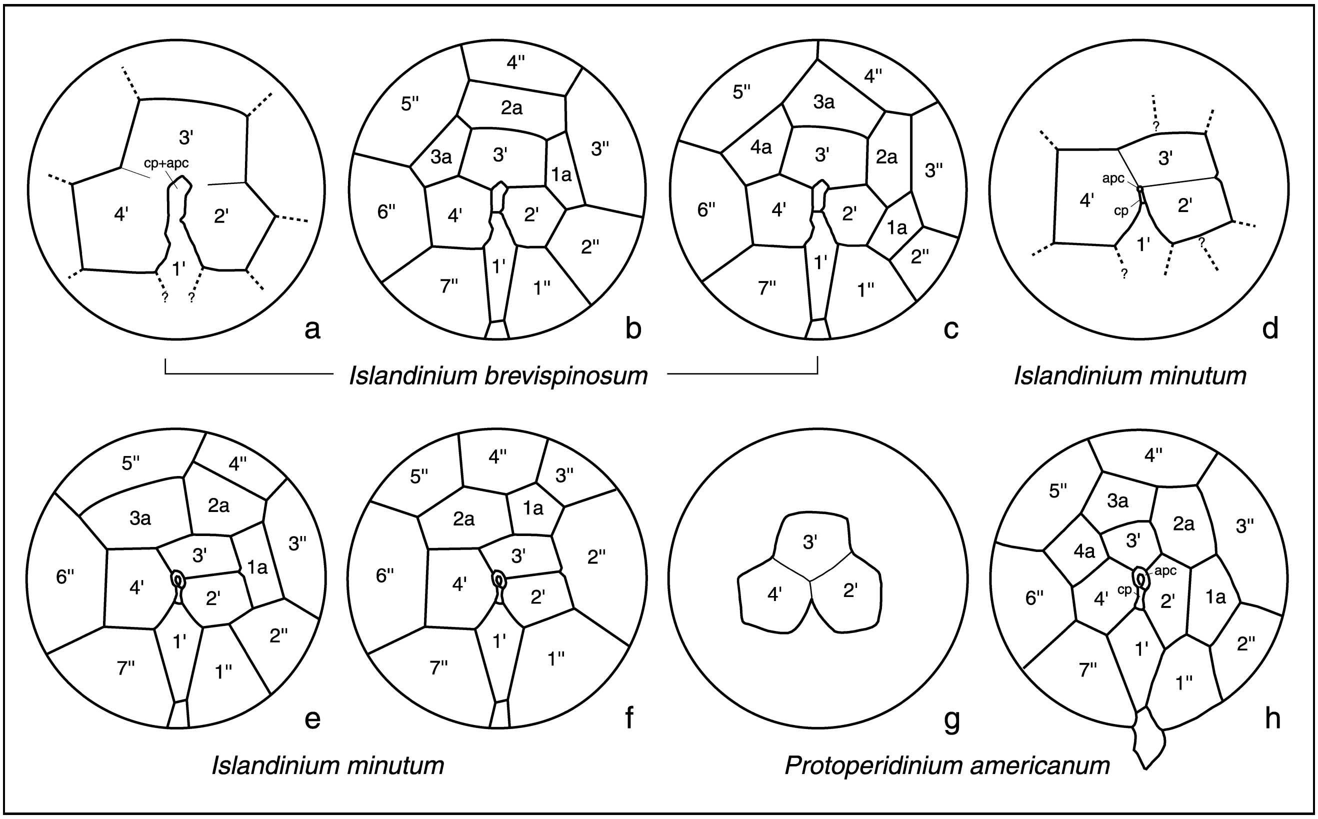

FIG. 6. Schematic episomal tabulation patterns of *Islandinium brevispinosum* sp. nov. and morphologically similar cysts with 3A apical archeopyles. (a–c) *Islandinium brevispinosum.* (a) 3A apical archeopyle (dashed lines indicate presumed adjoining plate boundaries) and (b, c) interpretations of the epitabulation involving either three (1a–3a) or four (1a–4a) anterior intercalary plates, respectively. Ortho-style tabulation is assumed but not observed (this study). (d–f) *Islandinium minutum* (Harland and Reid in Harland et al. 1980) Head et al., 2001. (d) 3A apical archeopyle (dashed lines indicate presumed adjoining plate boundaries) and (e, f) interpretations of the epitabulation involving either three (1a–3a) or two (1a–2a) anterior intercalary plates, respectively. Ortho-style tabulation is assumed (from Head et al. 2001). (g, h) *Protoperidinium americanum* (Gran and Braarud 1935) Balech, 1974. (g) Cyst with 3A apical archeopyle and (h) observed epitabulation from a motile cell showing four anterior intercalary plates and ortho-style tabulation (from Lewis and Dodge 1987). The abbreviations cp and apc represent canal plate and apical pore complex, respectively.

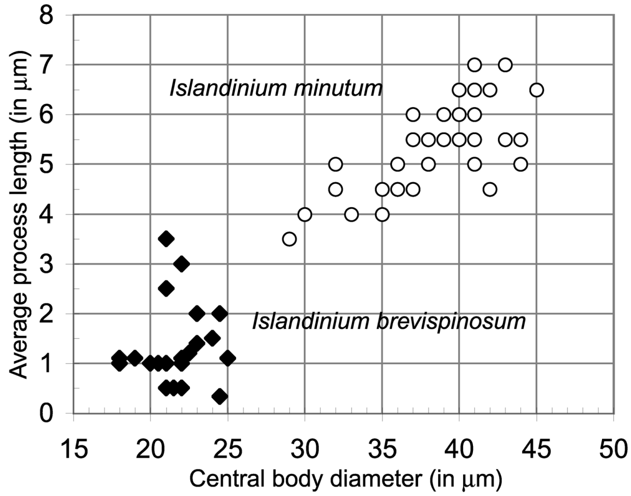

FIG. 7. Central body diameter vs. average process length for *Islandinium brevispinosum* sp. nov. (black diamonds) and *Islandinium minutum* (open circles; from the Kara Sea, based on Head et al. 2001). The two separate clusters demonstrate that size is a factor in distinguishing these species.

ples from three cores (Pospelova et al. 2002). Figure 2a shows the spatial distribution of *I. brevispinosum* and its proportion in dinoflagellate cyst assemblages from Apponagansett Bay, Clarks Cove, and New Bedford Harbor. *Islandinium brevispinosum* was encountered in all surface samples with its abundance ranging from 1% to 12% with the highest proportion in the outer part of Apponagansett Bay. All studied sites in Buzzards Bay are characterized by mean August water temperatures ranging from 23 to 25° C and salinities from 27 to 31 psu (Howes et al. 1999). Waters in this part of Buzzards Bay are considered to be nutrient rich, with the mean August nitrate concentrations 1.8 µM and phosphate 1.7 µM. (Howes et al. 1999).

In estuaries neighboring Buzzards Bay, Waquoit Bay, and adjacent Jehu Pond, *I. brevispinosum* was present and comprised 4% of total dinoflagellate cyst assemblages (Fig. 2b). These waters are characterized by a mean August temperature of 24° C and salinities ranging from 28 to 29 psu (Waquoit Bay National Estuarine Research Reserve). We do not have exact measurements of nutrient concentrations for Waquoit Bay and Jehu Pond waters, although it is known that these systems are also nutrient rich (Lamontagne and Valiela 1995).

The eight back-barrier lagoons of Rhode Island (Fig. 2c) are characterized by a range of mean August water temperatures and salinities from 19 to 23° C and from 5 to 29 psu, respectively (Lee et al. 1997). Cysts of *I. brevispinosum* were found only in Winnapaug Pond (1.5%; Fig. 2c), where mean August water temperature is 24° C, salinity 27 psu, concentrations of nitrates 2.0 µM, and phosphates 1.4 µM (Lee et al. 1997).

The presence of *I. brevispinosum* in the surface sediments of Narragansett Bay is inferred through our study of sediments from experimental tanks at the Marine Environmental Research Laboratory (University of Rhode Island) that originate from the central part of Narragansett Bay (Keller et al. 1999).

SUMMARY AND CONCLUSIONS

The large family Protoperidiniaceae contains only three extant species that are known with certainty to have apical archeopyles: *I. minutum* (the type of the genus), *I. brevispinosum,* and the cyst of *P. americanum* (which has no cyst-defined name). Head et al. (2001) suggested a biological affinity between *I. minutum* and the large motile-defined genus *Protoperidinium* but noted that the apical plates of *I. minutum* are arranged asymmetrically, whereas they are arranged symmetrically in the cyst of *P. americanum.* The apical plates in *I. brevispinosum* are relatively symmetrical in configuration, as with the cyst of *P. americanum,* and this adds support for an affinity between the genera *Islandinium* and *Protoperidinium.* A lack of accessory archeopyle sutures in *I. brevispinosum* prevents the total number of anterior intercalary plates from being determined, but three or even four are likely. *Islandinium brevispinosum* undoubtedly fossilizes, but neither fossils nor extant specimens have been reported previously. The small size, propensity to crumple, and unusual archeopyle style may have caused this species to be overlooked until now.

The genus *Islandinium* has been associated principally with modern high-latitude environments, where relative abundances may exceed 50%, although low abundances of *I. minutum* have been reported occasionally in mid-latitudes (Rochon et al. 1999, Head et al. 2001). The presence of *I. brevispinosum* with up to 12% relative abundance throughout the warm embayments of New England now extends the ecological range of this genus unquestionably into the warm-temperate zone.

Islandinium brevispinosum commonly occurs in shallow nutrient-rich estuarine waters that are generally characterized by mean August temperatures ranging from 23 to 25° C and salinities from 27 to 31 psu. It is possible that the presence/absence of this species in estuarine waters is regulated by this narrow range of temperature and salinity and by elevated nutrient content. Therefore this species may be of interest for environmental and paleoenvironmental reconstructions. Further studies of dinoflagellate cyst assemblages in estuarine systems on a larger scale will provide more detailed understanding of the ecology of *I. brevispinosum.*

Sediment samples were collected by members of the McGill Paleoenvironmental Laboratory and U.S. Environmental Protection Agency, and we thank G. L. Chmura (McGill University) and J. S. Latimer (U.S. Environmental Protection Agency, NHEERL, Atlantic Ecology Division) for provision of these samples. V. P. is grateful to G. L. Chmura for constant interest and encouragement. A. de Vernal generously made available technical facilities at the Université du Québec à Montréal (UQAM), and our study has benefited from useful discussions with A. de Vernal, M. Henry, and V. Loucheur (all UQAM). We thank the Waquoit Bay National Estuarine Research Reserve for providing us with data on water quality parameters in Waquoit Bay and Jehu Pond. H. V. Lovatt (New Hall, Cambridge) kindly translated the diagnosis into Latin. The work of V. P. was supported by a fellowship from the Natural Sciences and Engineering Research Council of Canada (NSERC), and M. J. H. acknowledges receipt of a Visiting Fellowship at Wolfson College, Cambridge. We are most grateful to the journal reviewers for their helpful comments.

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